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The influence of defoliation on regenerating aspen forest following burning

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Ronald E. Sosebee

External Examiner

Date...Dec. 21/81...............

The North-West - Canada.

O would ye hear, and would ye hear,
Of the windy wide North-West?
Faith! 'Tis a land as green as the sea,
That rolls as far and rolls as free,
With drifts of flowers, so many there be,
Where the cattle roam and rest.

..... Moira O'Neill

ABSTRACT

Aspen forests occupy an estimated 210,000 ha of the aspen parkland of western Canada. They also occur extensively in warmer environments of the boreal forest. Their replacement with grassland may increase beef carrying capacity in those regions.

Initial removal of trees invariably stimulates vigorous suckering from lateral roots. These suckers may be controlled by repeated top removal, but if herbicides or fire have been used for initial overstory removal, logs and stumps prevent subsequent control by mechanical means. Effectiveness of control with herbicides has been variable, with the more successful chemicals being potentially hazardous to user and environment, and the less successful ones requiring repeated application. The third alternative, fire, cannot be repeated frequently enough because insufficient fuel regenerates annually.

If aspen suckers could be removed by grazing with cattle, the foliage might then serve as a useful forage resource, and the control operation could be conducted without removing stumps and logs. Hence, the effect of season of grazing, age of stand, and the availability of alternative forages, on the utilization of aspen forest and its component species by cattle, was investigated. The effect of heavy grazing early or late in the growing season, on aspen forest succession following burning, and on the establishment of forage species, was examined also.

Since depletion of carbohydrates will reduce aspen suckering vigour, the effect of season of clipping on the concentration of root carbohydrates was determined, and the net balance between depletion of carbohydrates to support resprouting, and their restoration from subsequent photosynthesis, was studied in controlled conditions.

Cattle used aspen forest, as opposed to adjacent grassland, more readily late in the growing season than early. Within the forest, while sown forages were selected in preference to all other species, aspen was much more readily consumed late in the season than early.

Heavy grazing in late August practically eliminated aspen regeneration, and two quite different plant communities developed under the two grazing regimes. The early-grazed forest consisted of numerous clumps of aspen suckers interspersed with sown grasses and snowberry, while the late-grazed forest had very little aspen, but had more rose and snowberry and less sown grass.

Significantly fewer shoots arose from roots excised from the later clipped plots than from nil or early (July) clipped plots, though differences in root carbohydrate concentration were not detected. Carbohydrate in the parent roots in three different controlled light environments declined equally as shoots were produced, but shoots grown in light were heavier and produced more new roots than shoots grown in darkness. This suggests that new elongating shoots probably retain most of their photosynthates for top

growth, rather than replenishing reserves depleted in the production of those shoots.

Control of aspen suckers was not achieved by defoliation early in the growing season when carbohydrate levels were lowest. Investigations into the causes of suppression of aspen by August defoliation seem potentially rewarding.

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I. INTRODUCTION

Populus tremuloides Michx., hereinafter called "aspen", and also known as trembling or quaking aspen, or white or aspen poplar, is a slender deciduous tree reaching a height of 30 m in good growing conditions and having a smooth light green or whitish bark, which becomes furrowed and darker with age (Moss 1959).

Aspen Taxonomy

Aspen belongs to the family *Salicaceae*, the willows. Members of this family are dioecious trees with soft wood and bitter bark (Moss 1959). They bear leaves alternately on the stem. Flowers are borne in catkins (aments) without sepals or petals, and each flower in the catkin is borne singly in the axil of a bract or scale. Lester (1963) reported the occurrence of an occasional hermaphrodite catkin in 38% of the aspen trees he sampled. The numerous seeds bear tufts of hairs at their apices, those of *Populus* species being long and silky, enabling them to disperse over long distances (Maini 1972).

The genus *Populus* is characterised by the presence of several scales covering the winter buds. The catkins are relatively long and pendulous, and leaves are borne on long petioles.

P. tremuloides may be distinguished from most other *Populus* species by the characteristic flattened petioles bearing small leaves which are rounded at the base, and only slightly serrated (Maini 1968b). The flattened petioles tend to make movement occur in one plane, unlike trees with terete petioles whose leaves have more flexibility and consequently lie more steadily in the wind. The only other *Populus* species with flattened petioles is *P. sargentii* and it has larger cordate or deltoid leaves quite unlike those of *P. tremuloides*. Furthermore *P. sargentii* has very dark grey bark, especially on new growth, while *P. tremuloides* has light green or whitish bark (Moss 1959).

Distribution and ecology

Aspen is the most widely distributed tree in North America (Little 1971), stretching from Mexico to the Arctic Ocean, and from Nova Scotia to Alaska. It occurs throughout Western Canada (Figure I.1), its southern range being limited by low moisture and warm temperatures in south eastern Alberta and southern Saskatchewan (Moss 1944). To the north, aspen is an important component of the association known broadly as the Boreal Forest, where it forms part of the mixed-wood association with conifers, especially white spruce (*Picea glauca*) on well-drained uplands, and jack pine (*Pinus banksiana*) on sandy soils (Rowe 1959). In the mixed-wood association, aspen is either the dominant species in seral communities following disturbances such as fire, or a subdominant in a later successional stage dominated by the conifers (Moss 1955, Kranz and Linder 1973). Weaver and Clements (1938) described these associations as "fire sub-climax". Moss (1932) considered that the aspen/spruce association may be a climax

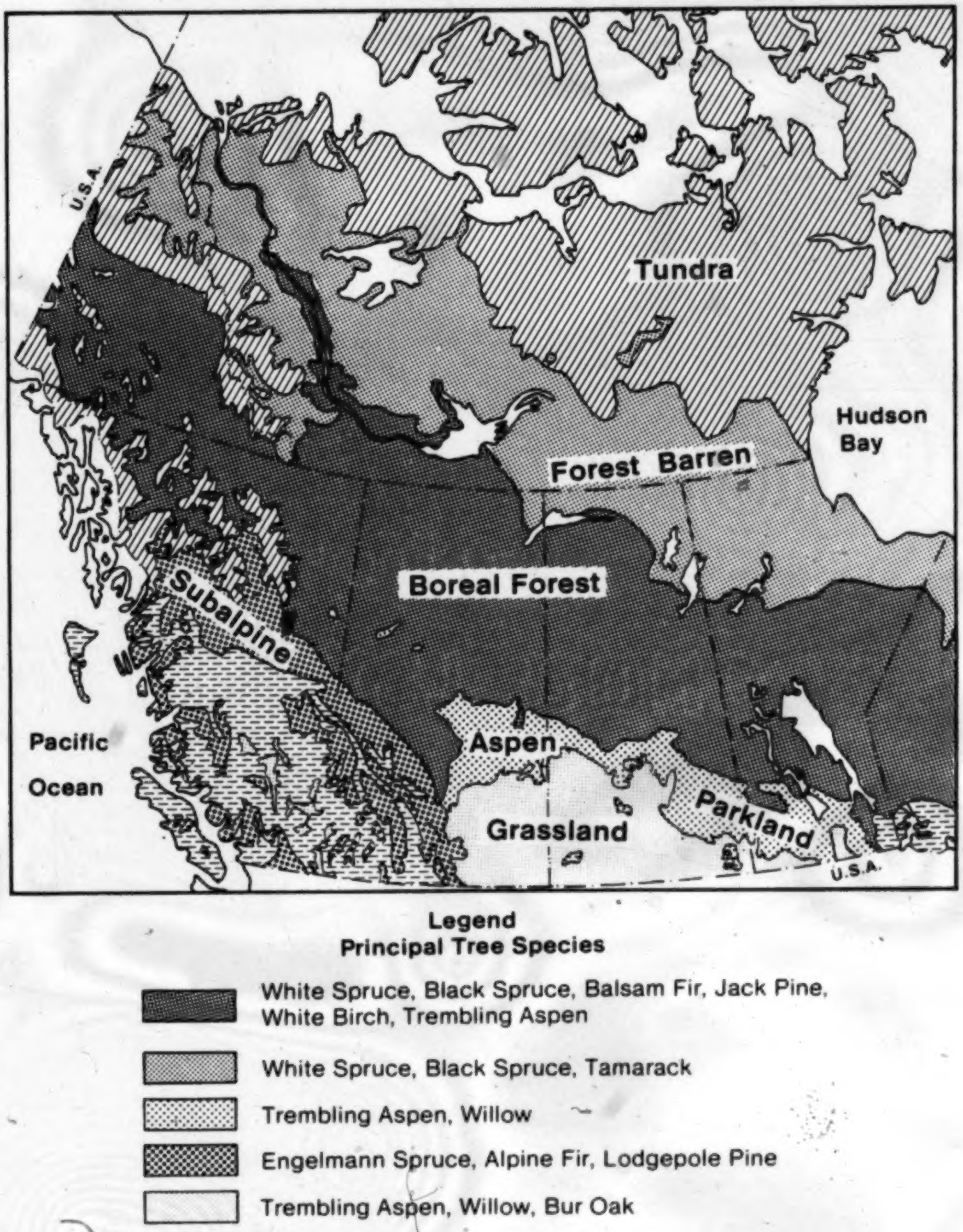
U.S.A.
Tundra
Hudson Bay
Forest Barren
Boreal Forest
Subalpine
Pacific Ocean
Aspen
Grassland
Parkland
U.S.A.
Legend
Principal Tree Species
White Spruce, Black Spruce, Balsam Fir, Jack Pine, White Birch, Trembling Aspen
White Spruce, Black Spruce, Tamarack
Trembling Aspen, Willow
Engelmann Spruce, Alpine Fir, Lodgepole Pine
Trembling Aspen, Willow, Bur Oak

Figure I.1 Major vegetation zones of Western Canada.

(Redrawn from Maini 1968a)

community in much of the drier southern portion of the mixed-wood zone. In this zone, aspen also occurs in association with balsam poplar (*Populus balsamifera*), or as a pure stand (Rowe 1959).

To the west in the foothills and slopes of the Rocky Mountains aspen is a common component of a complex range of plant associations, including Engelmann spruce, lodgepole pine, Douglas fir and others (Maini 1968a). In these associations, aspen is mainly an intermediate in the transition to the climax conifer community (Moss 1953, Rowe 1959). It forms a thin understory of stunted or spindly trees, largely shaded out by the larger dominant conifers. After a fire or logging operation aspen is the first tree to re-establish, because of its ability to sucker profusely. It assumes the role of a nurse crop or intermediate in the process of recovery and succession to the final climax conifer community (Hardy *et al.* 1976). Mueggler and Bartos (1977) actually recorded more conifer seedlings in upland Utah where there was an aspen overstory than where it was absent. They did not explain the effect but it may be that conifer seedlings establish more readily in the deep litter under aspen trees. Furthermore, competition from herbaceous species would be less severe under aspen.

Gradually, shade tolerant spruce saplings establish and, in time, grow through the aspen canopy. If the forest remains undisturbed, it will revert to dominance by the larger, taller conifers.

Further to the north, aspen continues to occur in warmer locations (south-facing slopes or river valleys) as a minor component of a community dominated by conifers (Rowe 1959). Here it is sparse and stunted, but may be an important source of winter browse for the ungulates of that region (Graham *et al.* 1963).

The transition between the mixed-wood association and the treeless grasslands to the south consists of a mosaic of groves of aspen, considered by Moss (1955) to be climax vegetation, alternating with fescue grassland, predominantly *Festuca hallii* and/or *Festuca doreana* (Looman and Best 1979). The grassland also includes *Stipa spartea* var. *curtiseta, Agropyron subsecundum, A. trachycaulum, Danthonia intermedia, Helictotrichon hookeri, Koeleria cristata* and a number of other grasses depending on environmental conditions. Moss and Campbell (1947) listed 20 grasses, 3 sedges, 10 shrubs, and about 115 forbs for this grassland.

This transition zone of aspen groves intermingled with grassland, being aesthetically pleasant, open, park-like country, is known in Canada as the aspen parkland. It extends from the Rocky Mountain foothills in southern Alberta in an arc through central Alberta and south central Saskatchewan to southern Manitoba, and occupies an estimated 14.5 million hectares in these provinces (Canada Census 1976). In Alberta alone, it occupies approximately 6 million hectares.

The forest groves in the parkland occupy the more moist sites in depressions or around sloughs and on north-facing slopes. Aspen grows, not in the poorly drained slough itself, but on the better drained slopes surrounding it. In south-eastern Alberta, shelter from hot, drying winds is a major factor in the distribution of aspen (Moss 1944). The grasses, which occur on the drier, more exposed sites on the tops of the hills and on south-facing slopes, occupy an increasing proportion of the area from the cooler moister forests in the north, to the open grasslands to the south.

Scheffler (1976) described the very predictable plant succession around a depression or a slough in the aspen parkland of central Alberta. The slough edge community may consist of halophytes, if saline, closely followed by a belt of willows (*Salix* spp.). If the depression or slough is not saline (a function of drainage), the lowest community may consist of sedges. The oldest trees of the aspen forest occur next in succession up the slope, followed by younger trees at the forest edge, beyond which there is a transition zone or ecotone, where aspen may be encroaching into grassland in an undisturbed situation. At the edge of the mature aspen grove lies a strip of grassland perhaps only 0.5 to 1 m wide. Beyond this is the *Symphoricarpos/Elaeagnus* community within which aspen suckers may be developing.

Among the understory shrubs growing in the shaded conditions in a mature aspen forest, are willow (*Salix*) spp., rose (*Rosa woodsii*), gooseberry (*Ribes oxycanthoides*), and raspberry (*Rubus strigosus*) (Scheffler 1976). There will be occasional aspen suckers, especially if there is a break in the canopy from storm damage or ageing. There may be some western snowberry (*Symphoricarpos occidentalis*). Commonly occurring herbs and forbs include *Aster laevis*, *Galium boreale*, *Pyrola asarifolia*, *Agropyron trachycaulum*, *Festuca scabrella*, *Lathyrus ochroleucus*, and *Vicia americana*.

At the forest edge, the species referred to above occur in greater profusion in a shrub community. The dominant shrubs are *Symphoricarpos occidentalis* and silverberry or wolf willow (*Elaeagnus commutata*), with accompanying shrubs *Amelanchier alnifolia*, *Prunus pennsylvanica* and *Prunus virginiana*. Moss (1932) included *Shepherdia canadensis*. Also present are the genera *Rosa*, *Rubus*, *Cornus*, *Solidago*, *Agropyron*, and *Festuca*, together with *Galium boreale* and *Lathyrus ochroleucus*.

Aspen is not restricted to any particular soil type, although it tends to invade the deeper, moister, black chernozemic soils first. Under aspen forest, soil fertility and organic matter decline, soil texture and colour become lighter, and the soil may be reclassified as a luvisol rather than a chernozem (Moss 1932, Scheffler 1976). Aspen grows satisfactorily on brown chernozems and may degrade them as well. Moss (1932) noted that the soils in the parkland are of the type which develop under grassland. He concluded that the presence of trees is a comparatively recent development, unlike further north where the glacial till has been degraded to the luvisols referred to locally as the "grey wooded" soils.

Moss (1932) described the aspen parkland as an area of interzonal tension - a large scale ecotone - and explained that the tension or competition is manifested along thousands of interfaces between forest and grassland communities. Like Scheffler (1976), Moss identified the transitional shrub community which occurs along this interface. Depending on conditions and management, especially the occurrence of fire in the grassland, the aspen forest may expand or remain stable in this ecotonal band around each forest grove.

Reproductive physiology

Reproduction by seed

Seed production in aspen is prolific in most years, although it may be almost absent in certain years (Moss 1938). Flowering age in *Populus* species is about 15 years, and a clone may be expected to produce good seed crops every second or third year (Maini 1968b). Seeds, being very light, are dispersed over great distances (1000 seeds with hair weigh 0.177g: Maini 1960).

Reproduction of aspen by seed is considered relatively rare in Western Canada (Moss 1938, Bird 1961), although Graham *et al.* (1963) reported widespread establishment of aspen by seed in Michigan. They agreed that establishment by seed was uncertain, requiring seed to be deposited in bare soil where favourable moisture and temperature conditions prevail for the few weeks required for germination and establishment.

Seeds remain viable for only a short period after their release, the period being shortened further by high humidity (Moss 1938), or high or fluctuating temperatures (McDonough 1979). Ironically, Moss (1938) found that conditions suitable for germination and survival of seedlings (warm and continually moist conditions) were the most unsuitable for the maintenance of viable seeds.

Vegetative reproduction

All aspen roots are capable of producing adventitious shoots at irregular intervals along their whole length in response to certain stimuli (Maini 1968b). These shoots are referred to as suckers in their first 3 or 4 years of growth, since, during that time, they remain largely dependent on the parent root. Suckers may be extremely prolific under some conditions, and are the main vehicle for vegetative reproduction. For example, in a 5 year old stand of aspen in Ontario, regeneration following clear cutting comprised 82% root suckers, 12% collar sprouts, and 6% stump sprouts (Maini 1968b). Bailey (1972) recorded 145,000 suckers ha^{-1} after mechanical clearing of an aspen grove in central Alberta. Bella and DeFranceschi (1972) recorded 175,000 suckers ha^{-1} after mechanical removal of trees in northern Saskatchewan.

Schier (1976) maintained that aspen has been able to remain a widespread and abundant species almost entirely because of its root suckering ability. This is perhaps, a little too strong, since aspen is so widespread, and has expanded rapidly in the prairies in the past eighty years (Moss 1955, Bird 1961, Bailey and Wroe 1974, Scheffler 1976, Johnston and Smoliak 1968). While much of this expansion may be attributed to suckering, movement over a wide area, such as the expansion in Manitoba from 1905 to 1956 (Bird 1961), must have involved more rapid spreading than is possible with suckering alone. Nevertheless, as noted by Moss (1938), Maini (1960), Bird (1961), and Graham *et al.* (1963), by far the greater proportion of aspen reproduction is by suckering.

Suckers are stimulated to develop by a disturbance such as fire, logging, or windfall. Without disturbance, suckers are produced at a lower but still significant rate. Schier and Smith (1979) recorded a mean of 8,300 suckers ha^{-1}yr^{-1} in an undisturbed forest over 4 years. Schier (1972) removed the apices of aspen suckers, and thereby stimulated the development of more suckers. He suggested that such suckering was triggered by a weakening of the inhibition exercised by existing shoots over primordia development (correlative inhibition), at times when top growth was inactive (e.g before bud swelling in spring) but when temperatures were high enough for metabolic activity in the roots.

Hormone control

Auxins, which inhibit primordia initiation (Eliasson 1961, Farmer 1962), are produced in the apical meristem (Eliasson 1969), and translocated basipetally to the root system (Eliasson 1972). Since auxin is rapidly inactivated (Eliasson 1971a,1972), the transport must be continuous in order to maintain levels in the roots sufficient to inhibit the initiation and development of shoots. Removal of the main stem by a disturbance, such as a fire or a logging operation, removes the source of auxin, thereby decreasing the concentration of auxin in the roots, enabling suckers to be initiated, or to develop from already initiated but suppressed primordia (Schier 1973b).

Cytokinins, which promote primordia initiation (Wolter 1968, Peterson 1975), are produced in the root tips (Feldman 1975, Peterson 1975, Skene 1975, Forsyth and Van Staden 1981). Removal of the main stem prevents translocation of cytokinins up the stem away from the root system, thereby raising their concentration in the roots, relative to auxin, and stimulating primordia initiation (Schier 1979).

Primordia may also be initiated in undisturbed forests when the rate of production of auxin at the tree apex is slowed. Such is the case during the dormant season or as the tree ages. Under these conditions the concentration of auxin in the roots usually declines, lowering the auxin:cytokinin ratio, and permitting the initiation of primordia.

In practise, the roots of aspen are nearly always well endowed with shoot primordia, suppressed or otherwise, even in undisturbed clones. (Brown 1935, Schier 1973a).

It should be noted that, in an undisturbed forest, primordia do not necessarily develop into suckers in the year in which they are initiated (Brown 1935). Schier (1973b) indicated that they frequently required another change in the auxin:cytokinin ratio to be reactivated at a later date. Alternatively, they may respond to changes in the levels of abscisic acid (ABA) or gibberellins (GA) (Schier 1973a), or to changes in carbohydrate concentration (Thorpe and Murashige 1970, Eliasson 1971b), or to changes in temperature (Maini and Horton 1966, Steneker 1974), or moisture (Scheffler 1976).

Direct evidence of seasonal changes in levels of GA in roots is not available. Gibberellins are synthesised both in young leaves and in root tips, with transport being non-polar (Moore 1979). In Alaska pea, GA was present in adequate quantities for growth during the exponential phase of growth, but not at very early seedling stage, or at maturity (Moore 1979). If the same relationship between the activity of the apical meristem, and GA concentration in the shoot, exists in aspen, the rate of synthesis of GA might increase during stem elongation in the first half of the growing season. Subsequently, it might decline in response to shortening days, as Railton and Wareing (1973) reported in potato leaves, to very low levels at senescence (Moore 1979). Bound forms may be released in late winter in response to environmental stimuli, as Eagles and Wareing (1964) found in birch.

Hence, the level of gibberellins (active form) in roots is likely to be low in the autumn and to increase in mid to late winter depending on ground temperature. Abscisic acid, which inhibits the growth of newly-initiated suckers, and reverses the effect of GA (Schier 1973c), is at relatively low levels in roots in autumn, winter, and spring, but reaches a peak concentration in mid-summer (Cohen *et al.* 1978). Thus, we might expect dormant season outgrowth of primordia to be restricted until the level of GA rises, coincident with low ABA concentration in late winter/early spring. Outgrowth will be accelerated when GA synthesis commences in earnest in the first half of the growing season, and may decline as GA declines in the latter half.

Carbohydrates

Aspen suckers are dependent on non-structural carbohydrates in the parent roots for both initiation of primordia (Thorpe and Murashige 1970, Eliasson 1971b), and some subsequent outgrowth (Tew 1970, Schier and Zasada 1973). The concentration of these carbohydrates is lowest immediately following leaf flush in spring, and reaches a peak in September (Tew 1970, Schier and Zasada 1973). Repeated removal of top growth, and consequent initiation and growth of new suckers, gradually reduces the vigour of regrowth of suckers (Berry and Stiell 1978, Perala 1974). Schier (1976) suggested that this was due to a gradual depletion of non-structural carbohydrates in parent roots. The decline in vigour is slow, suggesting either that only a small proportion of the amount in the roots is used in the production of a crop of suckers, or that some replenishment of carbohydrates was taking place between removal operations. Hence, the role of young suckers in root carbohydrate replenishment has important implications for brush control.

While shoots may be less dependent on root carbohydrates after emergence, they may not begin immediately to restore depleted reserves. Young aspen suckers may continue stem extension until early autumn (Kozlowski and Keller 1966), and , in doing so, use most current season photosynthates for apical growth. Young leaves (up to leaf 5) of *Populus deltoides* have a net import of carbon, and almost all carbon exported from these young leaves moves acropetally (Larson and Dickson 1973). Assimilate movement in branches of mature *Populus* species is mainly acropetal, at least until late June, when leaf expansion is practically complete (Donnelly 1974, Dickson 1977). After a late season defoliation, although generally initial root carbohydrate concentration would be high, there may be insufficient time for sucker development to reach the point of net basipetal photosynthate movement before leaf senescence, and plants would over-winter with a relatively low carbohydrate concentration. Suckers produced late in the growing season might not achieve frost hardiness before winter (Zehngraff 1946). In the following spring, the development of a further crop of suckers would entail further carbohydrate depletion. The relative depletion of carbohydrates, and the consequent suppression of suckering from defoliation at different times during the growing season, is important for optimal timing of control operations.

The problem of aspen encroachment

Since the settlement of western Canada by Europeans, and the consequent suppression of fires, conditions in the tension zone between forest and grassland have tended to favour aspen sucker survival (Moss 1932,1944). Consequently there has been a steady encroachment of aspen forest into the grassland. Bailey and Wroe (1974), working on Legal Land Surveys in Alberta, estimated the encroachment from 1907 to 1966 to be 3.2% of total area. Scheffler (1976) estimated that aspen occupies over 10% of the total surface area at Kinsella, Alberta, an estimated increase of 45.5% in 60 years. Johnston and Smoliak (1968) claimed an increase 0.75% per annum in the Cypress Hills of southern Alberta, although they presented no supporting data.

The aspen parkland in Alberta falls within the black and dark brown soil zones (Wyatt *et al.* 1944) and, as such, is good farming country if topography permits. However, much of it consists of "knob and kettle" topography, the result of glacial activity (Wyatt *et al.* 1944). Consequently, although soil and moisture conditions are suitable for farming, a large proportion of the area (32% in statistical divisions 6, 7, 8, 10 and 11) is used as native range, of which 11% or approximately 210,000 ha is woodland (Canada Census 1976).

Within the forest groves of the aspen parkland, herbage growth is limited by shading (Farmer 1963). Herbage yield under the forest canopy is very much poorer than in adjacent grassland (Table I.1).

Free-ranging cattle apparently tend to prefer grassland. Withih undisturbed forest in Alberta, Hilton and

Table I.1. Yield of herbage (kg ha^{-1}) in aspen forest and adjacent grassland communities in central (CA) and southern (SA) Alberta.

Grassland	Aspen forest	Site	Source
1944	154	CA	Bailey and Wroe 1974
2064	251	CA	Hilton and Bailey 1974
2009	304	CA	Hilton and Bailey 1974
1183	442	CA	Whysong and Bailey 1975
1200	400	SA	Johnston and Smoliak 1968

Bailey (1974) found that cattle grazed 92% of the relatively low yielding vetchling (*Lathyrus ochroleucus*), but grazed very little else. In the grassland, however, the average level of utilisation of all herbage was 42%. Cattle grazed undisturbed forest an average of only 17.5% of the time, from late June to mid August, the remainder being spent in grassland and sprayed forest (Hilton and Bailey 1972).

In Utah, Smith *et al.* (1972) recorded that cattle grazing in an enclosed area for about two weeks in late July over 3 years following a clear cut, used an average of only 3.3% of aspen sprouts, and this amounted to only 2% of the total weight of plant material of all species removed by cattle. Cattle (and deer) on open range removed 9.5% of available aspen.

Aspen forest, then is relatively poorly utilised by cattle. In view of the poor forage yields, and the poor level of utilization within aspen forest, the presence of aspen trees rather than grass on pastures in the aspen parkland, and perhaps, parts of the mixed-wood association, represents a serious economic loss, especially since the aspen groves usually occupy the more moist, and hence, potentially more productive sites in depressions or around sloughs.

The removal of trees and their replacement with useful forage species offers potential for increasing the carrying capacity of this range for beef cattle.

A. Brush control methods

A number of methods of clearing aspen are currently available.

Mechanical

Mechanical clearing in its various forms is probably the most popular commercial procedure for initial clearing. However, removal of the above-ground portion of the trees stimulates vigorous suckering. In fact, clear cutting is used by foresters to encourage aspen regeneration where this is desired (Jones 1975). Following clear cutting Sampson (1919) recorded 259,000 suckers ha^{-1} in Utah, Berry (1973) recorded 63,000 ha^{-1} in Ontario, and Perala (1979) recorded 75,000 ha^{-1} in Minnesota.

In Saskatchewan, Bowes (1975) recorded 47,000 stems ha^{-1} in country cleared by a bulldozer, disced twice, and sown to forages using a drill. In central Alberta, Bailey (1972) recorded 84,000 aspen suckers ha^{-1} following mechanical removal of the tree overstory, and 132,000 ha^{-1} where, in addition, the ground was disced twice. In north-central Alberta, Pringle *et al*. (1973) cleared aspen forest with a bulldozer, and recorded 43,000 suckers ha^{-1}, and 75,000 ha^{-1} where the ground was disced once as well.

It seems that the more mechanical disturbance the tree suffers over a short period, the greater the subsequent number of suckers which emerge. Schier (1976) contended that repeated removal of the top growth would eventually exhaust the carbohydrate reserves of the roots and bring about a decline in suckering vigour. There is some evidence to support this contention. Berry and Stiell (1978) reduced sucker density to 1.3% of initial density after 9 years by annual cutting in the dormant season. Perala (1979) required 7 years of annual winter cutting to achieve a similar measure of control.

Such repetition of mechanical operations is both laborious and expensive. Where the ground is being prepared for cash cropping, or even an intensive beef operation, the process of mechanical clearing and plowing, followed by repeated mowing, may be quite economic and certainly effective. Where the country is to be used as extensive cattle range, the total cost of forage establishment by mechanical means is unlikely to be recouped from increased returns from beef cattle. Furthermore, if herbicides or fire have been used for the initial overstory kill, the presence of dead and fallen timber prevents mowing or other mechanical operations to control suckers, and some alternative must be found to prevent rapid reversion to forest.

Herbicides

Herbicides would seem to be a realistic alternative to mechanical operations for controlling aspen. However, the published evidence available on the action of herbicides on mature trees is disappointing.

Hilton and Bailey (1974) achieved "little tree damage" from a light (1 or 2 kg ha^{-1} a.i.[1]) application of 2,4-D butyl ester, but heavier applications (3 - 4 kg ha^{-1} a.i.) stimulated suckering. A second application a year later at the same rate finally achieved some measure of kill at the 2 kg ha^{-1} rate and stimulated vigorous suckering, while at the 4 kg ha^{-1} rate there was an effective reduction in density of previously stimulated suckers.

Bailey and Anderson (1979) sprayed a young aspen/balsam poplar/willow community (average aspen height 8 m) with 2,4-D ester (2.2 kg ha^{-1} a.i.) and recorded a reduction in cover one month after treatment, but they found no significant change in aspen stem or sucker density.

Some degree of control, then, was recorded on some occasions, using heavy application rates. Stearman (Alberta Agric., personal communication) points out that 2,4-D and 2,4,5-T will only be effective if applied with large volumes of water. There should be enough water to achieve run-off from leaves. With mature trees this would require a prohibitively large volume, making aerial application impractical.

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[1] Active ingredient.

There has been more success reported on the effect of herbicides on sucker regrowth. Bailey (1972), using a single application of 2,4-D ester (2 kg ha^{-1} a.i.) one year after clearing and seeding an aspen forest, reduced sucker density by 40%. No further applications were made though they may very well have further controlled suckering. Sown alfalfa was eliminated.

Bowes (1975) achieved a 75% reduction in sucker number with 2 kg ha^{-1} a.i. of 2,4-D/2,4,5-T applied in June, two years after clearing, discing, and sowing to forages. A second application the following June reduced sucker density a further 15%. However, about 200 stems ha^{-1} remained, and this would leave sufficient live roots for the area to eventually revert to forest unless some further control operations were undertaken.

Very little 2,4-D applied to the leaves of aspen is translocated to the root system, even if the application is just prior to leaf fall (Eliasson and Hallmen 1973). Apparently the chemical is readily transferred from the phloem to the xylem and transported acropetally. Thus it tends to concentrate in the apex, with very little reaching the root system, which may explain, in part, why its action is not more permanent.

Bowes (1976) used a 2,4-D/picloram mix two years after clearing and sowing, and found that aspen shoot number declined 43% more after one application than without it. Sown alfalfa was completely eliminated. Almost 3000 aspen stems had remained, and control operations of some sort would have to be maintained to prevent reversion to forest.

In another experiment, Bowes (1978) applied a 2,4-D/2,4,5-T mix to aspen regrowth in a brome/alfalfa pasture and measured only 35% reduction in aspen cover compared with untreated plots two years later. A 2,4-D/dicamba mix reduced cover by 60% and a 2,4-D/picloram mix reduced it by 89%. He did not describe persistence of the alfalfa, which had been sown after the initial mechanical clearing operation, fared, but little survival seems likely. Further control measures would be required to prevent reversion to forest.

The cost of repeated applications of herbicide may be substantial, since they would probably have to be made from the air, unless the trees and logs were removed by mechanical means. Furthermore, herbicides are frequently subject to restrictions associated with chemical residue. Picloram is, at present, restricted in its use until more evidence is available on its persistence in the environment and its movement in the food chain of man and beast. At present, use of 2,4,5-T for aspen control is illegal in Alberta and Saskatchewan. Application of any of these brush control chemicals would undoubtedly eliminate all trace of alfalfa and other herbaceous legumes.

In general, the action of herbicides on mature trees is uncertain, being limited either by solvent volume, or by environmental hazards. On sucker regrowth, some measure of control may be expected from the use of a 2,4-D/2,4,5-T mix, and even better control from a 2,4-D/picloram mix if it is not environmentally hazardous, but at least two applications are required, and probably more follow-up operations after that.

Burning

Fire can be used for a variety of management purposes. Indians practiced spring burning of prairie grassland to improve the quality of feed available to bison, thereby concentrating them and facilitating hunting (Nelson and England 1971). Prescribed burning has been widely used by land managers to regenerate decadent stands of aspen (Sampson 1919, Perala 1972, Bartos and Mueggler 1981). Prescribed burning is recommended by foresters to re-establish aspen stands after harvest in cases where complete clearcutting is not possible (Perala 1974, DeByle 1976).

These applications have the common objective of promoting suckering by achieving a total kill of above-ground vegetation. For permanent removal of aspen, such an operation must be followed by further control treatments. Some success has been achieved with repeated burning.

In Minnesota, Buckman and Blankenship (1965) achieved a 94% decline in sucker density in 4 years by repeated burning in early spring before the onset of the growing season.

Likewise, Perala (1974) reported a decline in sucker number following burning in spring before leaf flush. His burning operations were conducted every second year. He pointed out that, generally, burning operations cannot be repeated annually or even biennally in aspen forest due to lack of fuel. Certainly, this is the experience in Alberta (Bailey, personal communication).

Following initial burning, then, a different process for top growth control is necessary.

Grazing

Early workers in the aspen forest communities of North America were aware of the impact of cattle on aspen regeneration. Sampson (1919) reported that cattle browsed up to 36% of the aspen suckers in standing timber, and 20% of suckers emerging after a clear cut.

Moss (1932) considered that continual browsing by cattle would prevent aspen regeneration in the aspen parkland of western Canada, but he presented no supporting evidence.

In Utah, Smith *et al.* (1972) measured 22% mortality of suckers attributable to the presence of cattle, in an aspen forest one year after clear cutting, 10% in the second year, but none in the third year. Cattle selected more aspen on open range than in controlled grazing enclosures.

In the aspen parkland of Alberta, cattle with access to forest treated with herbicide, and to open grassland, removed at least some leaves from an average of 20% of available aspen suckers in the forest, but the range of use between different sites varied from 3% to 43% (Hilton and Bailey 1974).

The reason for the variation in utilisation in the reported studies is not clear. The level of available alternative forage has a marked influence on diet selection (Heady 1964). However, in the study by Smith *et al.* (1972), there would have been a wider range, and greater quantities, of alternative forage species on open range, than in areas of controlled grazing. This would have led to selection of less aspen on open range than under controlled grazing, unless, in fact, animals were grazing aspen preferentially. Smith *et al.* (1972) only provided herbage yield data averaged over three years and, although no measure of error was reported, the available herbage in the controlled grazing and open range areas (937 and 868 kg ha^{-1}) was not significantly different in biological terms. In Hilton and Bailey's (1974) study, differences in available herbage were small and varied positively with aspen utilization.

Some variation in the acceptability of aspen suckers to cattle may arise from genetic differences in plant palatability. Clonal (genetic) variation in aspen is important in many other characteristics, e.g. suckering (Schier 1974), growth and maturation (Barnes 1966), carbohydrate reserves (Schier and Johnston 1971), and decay (Wall 1971). Palatability may be influenced by the age of the foliage (Heady 1964). Brundage and Branton (1967) demonstrated changes in diet selection by cattle over a season as the various species matured at different rates. In the studies of Hilton and Bailey (1974) and Smith *et al.* (1972) sampling took place relatively late in the season (mainly July) when variation in sucker age would add to plot variation and contribute to sampling error. Smith *et al.* (1972) observed that selection of aspen in open range increased as the season progressed from spring to autumn.

Recently, Bryant and Kuropat (1980) established a strong negative correlation between the plant species selected by moose (*Alces alces*) and their "resin content", resin being defined as consisting largely of terpenes and phenolic resins. They concluded that animals select mature current growth against younger new growth, the latter being high in resins. This is consistent with the observations of Smith *et al.* (1972) and may explain, in part at least, why the palatability of the aspen suckers seemed to change through the growing season.

It would seem that the selection of aspen suckers by cattle is highly variable, and that the causes of variation are poorly defined. With more information about the factors influencing the selection of aspen by cattle, grazing might well serve as a useful low-cost adjunct to other brush control operations, especially where logs and stumps prevent mechanical operations, and where cost is a limiting factor. Use of the grazing animal to remove regrowth offers the added advantage that the vegetable matter produced in the regenerating forest becomes a forage resource rather than simply being destroyed.

B. Experimental objectives

If cattle are to be considered as a possible aid to the control of aspen suckers, it is necessary to determine the factors which influence the extent to which they will utilize them.

If clearing operations are to be of any lasting benefit to livestock producers, the trees have to be replaced by useful forage species. Preliminary results indicate that forage seeds will germinate in the ash following a fire, but that seedlings are unable to compete with regenerating brush species (Bailey, personal communication). Heavy grazing may reduce competition from regenerating brush species, and enhance forage seedling establishment and survival.

The timing of regrowth control operations, including grazing, has received scant attention in the literature. Canada Agriculture recommends that control operations be carried out in spring, to coincide with the time of lowest carbohydrate reserves (Friesen *et al.* 1965). Such timing was expected to exhaust energy reserves faster than at other times of the year, and to lead to the most rapid decline in suckering vigour. However, the net balance between carbohydrate depletion from outgrowth of suckers, and carbohydrate replenishment from emerged and photosynthesising regrowth, was not known.

Therefore, an experiment was conducted to determine:

1. The selection of aspen by cattle as influenced by season of grazing, age of stand, and the availability of alternative forages.
2. The effect of heavy grazing early or late in the growing season on:
    a. aspen forest succession following burning,
    b. the establishment of broadcast forage species.

A second experiment was conducted to establish the effect of clipping at various times during the season on root carbohydrate levels at the end of the season, and then to separate the effect into:

1. decline in non-structural root carbohydrates (TNC) due to shoot development,
2. TNC replenishment due to subsequent shoot photosynthesis,
3. the effect of the subdominant suckers, growing in shade, on TNC replenishment.

C. Experimental site

The field experiments were conducted on the University of Alberta Ranch at Kinsella in the aspen parkland of Alberta (approximate latitude 53 02'N, longitude 111 33'W), at an elevation of between 700 and 900 m above sea level.

Wonders (1969) classified the area as "dry subhumid". The climate is characterised by cold winters and mild dry summers. Average annual precipitation is 432 mm of which 75% or 323 mm falls in the growing season from April to September inclusive. The standard deviation for growing season precipitation is 99 mm, based on records for 19 years. Generally precipitation at Kinsella falls as rain from April to November, and as snow from December to April, with frequent exceptions. Average monthly precipitation as recorded at the University of Alberta Ranch from 1962 to 1980 is presented in Table I.2, together with monthly precipitation for the period of experimentation. The weather station was approximately 3 km east of the site of the field studies. Mean monthly temperatures (records over 19 years), and temperatures for the experimental period are presented in Table I.3. The normal frost-free period is 100-120 days from mid to late May to early September (Wonders 1969). Evapotranspiration in central Alberta averages from 120 to 180 mm per annum (Wonders 1969).

The experiments were located on strongly undulating country described by Wyatt *et al.* (1944) as part of the Viking moraine left by the Keewatin ice sheet 15,000 years ago, and having "frequent rolls and kettle holes" with "many sloughs and lakes". Wyatt *et al.* (1944) classified the soils as unsorted glacial loams with an average of 7-10 cm of black topsoil. Profile depth and texture vary in a catena from heavy and shallow on the knolls to relatively deep and

Table I.2 Monthly precipitation (mm) at Kinsella from 1979 to July 1981, and the monthly average (19 years).

	1979	1980	1981	1962-80 av.
January	10.6	26.5	4.0	24.1
February	28.3	17.2	4.7	16.2
March	13.6	32.6	8.4	17.6
April	15.7	4.9	27.5	17.8
May	2.6	51.4	10.0	45.0
June	46.5	179.1	29.3	77.9
July	120.2	119.3	53.5	86.4
August	34.7	123.2		58.5
September	55.0	30.5		37.3
October	4.2	16.2		15.3
November	3.7	4.3		15.1
December	17.1	33.9		20.3
Total	355.2	639.1		431.5

Table I.3 Mean monthly maximum and minimum temperatures (°C) in 1979, 1980, and the 1962-80 average.

	1979		1980		1962-80 AV.	
	MAX.	MIN.	MAX.	MIN.	MAX.	MIN.
January	-12.1	-20.7	-10.7	-20.6	-14.0	-21.0
February	-19.3	-28.3	-3.5	-15.0	-7.7	-15.8
March	2.6	-8.7	-1.6	-12.6	-1.7	-10.7
April	4.0	-4.0	16.0	2.1	8.0	-0.6
May	14.0	4.0	20.6	5.4	16.1	6.3
June	20.0	10.0	20.6	9.7	19.9	10.4
July	23.0	13.0	23.2	10.0	21.9	12.5
August	22.0	10.0	18.9	7.9	21.6	10.8
September	18.0	7.0	16.8	4.0	15.3	5.8
October	11.7	2.3	13.8	1.3	9.7	1.0
November	-2.1	-8.9	5.1	-4.7	-1.7	-8.7
December	-9.9	-15.5	-10.3	-19.7	-9.9	-15.7

friable in the valleys. The calcium horizon occurs at a depth of from 40 to 60 cm. These soils are known broadly as black chernozems.

II. INDIRECT ESTIMATION OF WOODY PLANT BIOMASS

A. Introduction

In order to estimate changes in the relative preference of cattle for the major woody plants in the aspen forest, the weight of material of each species present had to be determined each day through the grazing period.

The most direct method of determining weight of the above-ground material is by destructive sampling, drying, and weighing. However, as Rutherford (1979) points out in his review of the subject, the process has a number of important drawbacks:

1. Firstly, woody shrub communities tend to be highly variable, and usually, at least 15 samples per plot or community are required to minimise the standard deviation. The larger the area to be sampled, the greater the variation encompassed, and the more samples which are required. Usually it is useful to stratify into sub-communities, and this involves more sampling.
2. Secondly, with small plots on which estimates must be made daily, the destruction of plants by sampling may eventually have a substantial impact on the plant community and mask or bias treatment effects.

For this reason, destructive sampling was not considered compatible with the studies reported in Chapters III and V. In the latter study, an estimate was required of the total dry matter of each species each day as the grazing period progressed from 0 to 10 days or thereabouts. Furthermore, because variation in the shrub community was expected to be large, it was considered useful to estimate changes on the same fixed sample areas, a technique only possible with non-destructive sampling.

A number of techniques have been developed for non-destructive estimation of the available browse and the amount removed by browsing animals. The most rapid is the twig count method as tested by Jensen and Scotter (1977). This method merely provides an estimate of proportional utilisation without providing an estimate of biomass. Jensen and Scotter (1977) compared twig count and twig length estimates of utilisation, and found a reasonable relationship at low levels of utilisation (r^2=0.8) but only a very poor relationship at heavy levels of utilisation. The twig count seems more useful if combined with other measurements.

Shafer (1963) devised a function for converting twig numbers to total weight of browse, based on the average weight of browsed twigs as estimated by clipping. The length of twig clipped was based on the average diameter of browsed twigs. Since the twig weight estimate depended on a particular intensity of browsing for estimation of the appropriate mean diameter of browsed twigs, the system is satisfactory for range inventory studies but is not satisfactory where it is desired to measure the effects of changes in browsing intensity.

Schuster (1965) used length as an estimator of weight in combination with twig number and explained between 74% and 97% of variation depending on species. He found that twig length was the single variable most closely correlated with both shoot and twig weight. Stem diameter was less well correlated with weight.

Basile and Hutchings (1966) found a reasonable relationship between the diameter of bitterbrush twigs and their dry weight (r^2=0.89) and between twig length and dry weight (r^2=0.87). When both diameter and length were used, they obtained an r^2 of 0.95.

Rutherford (1979) listed a number of studies in which good relationships were established between diameter and/or length and weight of browsed twigs including one on aspen (Telfer and Cairns 1978).

All of this work has centred on the estimation of browse rather than total biomass. Allometric estimation of biomass of the whole aerial portions of the plants has usually involved the same parameters as those used in twig estimation, particularly diameter. Perala (1973) developed stand equations for estimating aerial biomass of aspen based on the square of the tree diameter at breast height (DBH) multiplied by the height. These equations explained 99% of variation.

This predictive parameter has been widely used in forestry circles (Berry 1973, Bella and De Franceschi 1980). Bartos and Johnston (1978) achieved a good prediction

(r^2=0.997) using DBH only. This had obvious advantages for use in field estimations, but, as with all these equations, was site-specific. Koerper and Richardson (1980) found that DBH was a good predicter of the woody portion of the tree (r^2>.94) but was less reliable for leaves and new growth. Addition of height improved this estimate, especially between sites. However, they pointed out that height estimates were prone to too much error for them to reduce the confidence interval for the regression, and direct measurement of height is usually impractical.

In general then, foresters have selected the measurement that is most convenient to them, while still providing a satisfactory estimate.

In the experiment reported here on aspen suckers, a height measurement was much more convenient than a diameter measurement. Plant height has been used as the predictor much more rarely. Kelly and Walker (1976) used it to measure seasonal growth of the Zimbabwean tree *Colophospermum mopane* (r^2=0.72), and with the shrub *Combretum apiculatum* (r^2=0.86). With other species, the best regression involved volume or diameter parameters as well.

It seemed that the best estimator of weight from non-destructive sampling would be derived from a combination of height and diameter. Daily measurement of height and stem diameter was attempted but found to be too time consuming.

If a single measurement had to be chosen it had to give an indication of the extent of browsing. If plant height was measured before grazing, then the decline in plant height could be used as such an indication if a good relationship could be established between plant length and plant weight. A measurement of basal diameter would give no indication of browsing, and a diameter measurement of browsed stems was far too time consuming.

With single-stemmed suckers in their first and second year of growth one might expect a length measure to be akin to the twig length measure which was found adequate by Schuster (1965) and Basile and Hutchings (1966). Consequently, it was decided to base estimates on a measurement of the changing height of each plant within fixed quadrats.

In this experiment, a predictive estimation of the dry weight of the four major woody species of the regenerating aspen forest was developed from plant height, for unbrowsed and subsequently browsed plants. Daily measurements of height of these species were made within randomly located quadrats, the position of which was fixed to allow repeated daily measurements.

The estimation of weight of plant material from these height measurements was derived from the sampling of these major species in regenerating forest adjacent to, and treated identically to, the experimental paddocks. The relationships developed were needed to estimate the weight of browsed plants as well as entire plants. Hence, relationship between height of browsed plants and their weight involved a special adaptation of the direct regression of height on weight.

B. Methods

In 1979, concurrent with the grazing of both the early- and late-grazed treatments, a sample of the aerial portions of 100 plants each of aspen, rose, raspberry, and snowberry were randomly collected from regenerating forest adjacent to the experimental paddocks. These sampled areas had been treated identically to the experimental areas prior to grazing.

The samples were taken to the laboratory and frozen. Some months later they were thawed and 40 of each were cut into six sections, oven dried at 65°C for 24 hours and weighed. The portions consisted of the lower 50% of the stem divided into two equal portions (25% each), and four equal portions of the upper 50% (12.5% each) which allowed a cumulative determination of the weight of 25% of the height,50%, 62.5%, 75%, 87.5%, and full height.

The standard deviation of weight of the full height based on 40 plants was not reduced by using the remaining 60 plants of the original sampling. Hence only the 40 sectioned plants were used in determining the height: weight relationships.

The regressions which best fitted the relationship between full height and weight were quadratic polynomials forced through the origin. This form of regression was also the best fit for regressions of proportions of height and equivalent weight. For each species, the coefficients from these regressions were plotted against proportion of height. Regressions (third degree polynomials) fitted to these points could then be used to determine the appropriate coefficients for insertion into the original height:weight regression for that species. In this way it was possible to calculate the weight of a species at full height, or portion thereof.

In 1980, plants inside the experimental area had been grazed, so that they were morphologically unlike the ungrazed plants growing outside. Hence, it was not possible to get samples of regrowth of rose or raspberry, outside, and sampling inside the paddocks for these now relatively rare but preferred species was considered likely to have too much impact on the plant community and to lead to bias in both grazing behaviour and plant succession. Aspen, however, could be sampled in June in the early-grazed plots because it was abundant. Late-grazed aspen was also estimated from this June sampling.

For rose in 1980, the relationship established in late 1979 was considered adequate because by that time the plants were relatively mature with an established woody portion. Rose plants in 1980 had a similar structure.

The structure of raspberry plants in 1980 was similar to newly emerging plants, since top removal during the previous season had killed top growth, which resulted in new shoots emerging from rhizomes below the ground (see Chapter III). Growth and development was slow, and hence, the relationship for early 1979 was considered the most appropriate.

Snowberry, in 1980, was similar in structure to snowberry at the end of the 1979 growing season.

For comparison with height/density estimates, a direct estimate of total woody plant biomass was made concurrently with height and density measurements by harvesting all plant material within 0.5 m^2 quadrats. There were 10 quadrats per plot (30 per treatment) paired with the density and height observation sites.

C. Results

The regression equations which best fitted the relationship between height and weight are presented in Tables II.1, II.2, II.3 and II.4 which show coefficients and r^2 values.

The relationships between these coefficients (b_1 and b_2) and percent height for each species at each sampling time were best described by third degree polynomials shown in Tables II.5 and II.6.

Given the unbrowsed height (H) of a plant, these regression equations could be used to predict the appropriate b values for use in the quadratic equation

$$W = b_1 H + b_2 H^2$$

which was the best estimator of W (plant weight)(Tables

II.1-II.4).

Observations of grazed plants in the selection study (Chapter V) included measurement of the initial height and subsequent browsed height of the aspen, rose, raspberry and snowberry. By means of an *APL* computer programme (Appendix B) the average height of a species was calculated as a percent of initial height (step 8) and *b* values for that species (established in steps 20 to 21) used to predict weight in grams per plant of those species (step 23). The appropriate *b* values were added by hand to the matrix of data being transformed.

D. Discussion

In Table II.7 a comparison can be made of the estimates of weight of woody species from height/density measurement and the estimate from direct harvesting. The table illustrates the variability associated with the direct harvesting technique for biomass estimation. In no case are the two approaches significantly different, but the trend of overestimation by clipping or underestimation by height measurement is apparent and consistent. The relationships between the estimations at different dates are consistent, and it is the comparative aspect of the estimations that is important for establishing relative preferences.

Table II.1 Regression coefficients for linear quadratic regressions which pass through the origin, for proportion of height (%H) on its equivalent weight, for aspen sampled 3 times in 1979/80.

Sample	%H	Regression coefficients b_1	b_2	r^2
1979 Early	100	-.0178	.0020	.92
	87.5	-.0195	.0020	.92
	75	-.0208	.0019	.92
	62.5	-.0211	.0017	.91
	50	-.0193	.0015	.90
	25	-.0081	.0007	.85
1979 Late	100	-.1292	.0035	.96
	87.5	-.1380	.0035	.97
	75	-.1373	.0033	.97
	62.5	-.1271	.0029	.96
	50	-.1056	.0024	.96
	25	-.0583	.0012	.95
1980 Early	100	-.1036	.0048	.94
	87.5	-.1228	.0050	.95
	75	-.1244	.0047	.96
	62.5	-.1220	.0042	.95
	50	-.1097	.0034	.93
	25	-.0599	.0017	.90

Table II.2 Regression coefficients for linear quadratic regressions which pass through the origin, for proportion of height (%H) on its equivalent weight, for rose sampled early or late in 1979.

Sample	%H	Regression coefficients b_1	b_2	r^2
Early	100	-.0116	.0018	.96
	87.5	-.0191	.0017	.96
	75	-.0199	.0015	.96
	62.5	-.0234	.0014	.95
	50	-.0195	.0011	.95
	25	-.0085	.0005	.96
Late	100	-.0387	.0026	.87
	87.5	-.0373	.0024	.86
	75	-.0371	.0022	.86
	62.5	-.0335	.0020	.85
	50	-.0294	.0016	.82
	25	-.0226	.0009	.73

Table II.3 Regression coefficients for linear quadratic regressions which pass through the origin, for proportion of height (%H) on its equivalent weight, for raspberry sampled early or late in 1979.

		Regression coefficients		
Sample	%H	b_1	b_2	r^2
Early	100	-.0121	.0024	.88
	87.5	-.0199	.0024	.88
	75	-.0226	.0023	.87
	62.5	-.0168	.0018	.85
	50	-.0118	.0014	.85
	25	-.0054	.0006	.81
Late	100	-.0877	.0031	.88
	87.5	-.0928	.0029	.87
	75	-.0857	.0026	.85
	62.5	-.0769	.0022	.83
	50	-.0589	.0017	.82
	25	-.0198	.0006	.79

Table II.4 Regression coefficients for linear quadratic regressions which pass through the origin, for proportion of height (%H) on its equivalent weight, for snowberry sampled early or late in 1979.

		Regression coefficients		
Sample	%H	b_1	b_2	r^2
Early	100	-.0043	.0016	.89
	87.5	-.0091	.0015	.88
	75	-.0075	.0013	.88
	62.5	-.0042	.0010	.85
	50	.0001	.0007	.84
	25	-.00003	.0003	.86
Late	100	.0327	.0004	.89
	87.5	.0054	.0007	.90
	75	-.0174	.0010	.89
	62.5	-.0168	.0009	.89
	50	-.0190	.0008	.89
	25	-.0083	.0004	.89

Table II.5 Coefficients for regressions of b_1 values from height:weight quadratic regressions on percent height, for aspen sampled 3 times, and rose, raspberry, and snowberry sampled twice each.

Spp.	Sample		Regression coefficients				
			a	b_1	b_2	b_3	r^2
Aspen	1979	Early	.0183	.1431	.1637	-.0568	.99
		Late	-.0115	-.1549	-.1801	.2178	.99
	1980	Early	.0128	-.3287	.1289	.0827	.99
Rose	1979	Early	.0121	-.1001	.0703	.0058	.96
		Late	-.0186	-.0040	-.0573	.0415	.99
Rasp.	1979	Early	-.0261	.1677	-.4012	.2476	.99
		Late	.0158	-.1138	-.1559	.1660	.99
Snowb.	1979	Early	-.0280	.1935	-.3792	.2093	.99
		Late	-.0111	.0732	-.3215	.2927	.98

Table II.6 Coefficients for regressions of b_2 values from height:weight quadratic regressions on percent height, for aspen sampled 3 times, and rose, raspberry, and snowberry sampled twice each.

Spp.	Sample		Regression coefficients				
			a	b_1	b_2	b_3	r^2
Aspen	1979	Early	-.0005	.0056	-.0037	.0005	.99
		Late	.0001	.0038	.0037	-.0041	.99
	1980	Early	.0005	.0028	.0108	-.0093	.99
Rose	1979	Early	-.0004	.0039	-.0020	.0002	.99
		Late	-.0000	.0039	-.0011	-.0002	.99
Rasp.	1979	Early	.0006	-.0027	.0124	-.0080	.99
		Late	-.0005	.0045	.0010	-.0018	.99
Snowb.	1979	Early	.0005	-.0026	.0086	-.0048	.99
		Late	.0001	.0005	.0038	-.0041	.97

Table II.7 Biomass (kg ha^{-1}) of woody species at two grazing times in 1979 and 1980, estimated from height/density and from direct clipping, showing 95% confidence intervals.

	Estimation type	
	Height/density	Clipping
1979 Early	445 ±91	1186 ±774
1979 Late	3103 ±186	4125 ±1183
1980 Early	824 ±90	1242 ±569
1980 Late	1453 ±147	1610 ±684

III. EFFECTS OF GRAZING ON REGENERATING ASPEN FOREST

A range of aspen brush control methods and frequencies have been investigated, but the only work on season of operation has been conducted by foresters wishing to promote suckering of aspen. They have concluded that clear cutting in the dormant season should stimulate more suckers than cutting in spring or summer, early or late (Zehngraff 1946, Stoeckeler and Macon 1956). For brush control, the timing of top kill has not been systematically investigated.

Competition from vigorous grasses may aid in control of aspen suckers. Bailey (1972) recorded less aspen regrowth where cleared and ploughed ground was sown to alfalfa and bromegrass. Furthermore, if aspen is to be cleared to improve the rangeland for beef cattle, it must be replaced with useful forage species. Preliminary attempts to establish forages by broadcast seeding after fire in aspen forest indicated that the method may be effective, providing competition from brush regrowth can be controlled (Bailey 1978). This technique was employed in the field studies reported here.

The experiment reported in this chapter was to determine the effect of time (i.e. season) of heavy grazing by cattle on the growth and botanical composition of a regenerating aspen forest seeded to forage species following burning.

In the experiment, the effect of defoliation at the time of minimum carbohydrate was compared with defoliation just prior to leaf fall, when carbohydrate is high (Schier and Zasada 1973), but when no time remains for carbohydrate replenishment before the dormant season.

A. Methods

Experimental design

A mature aspen forest at Kinsella was burned in May 1972 and the seven year old regrowth burned again 15th May 1979. All top growth within the experimental area was killed by the fire. Prior to burning in 1979, trees were about 3-4 m high, with an average DBH[3] of 2.0 ±0.3 cm. Aspen density was estimated at 23,100 ±8,300 ha^{-1}. Such a stand would correspond to a stand on a relatively good site in the mixed-wood section of the boreal forest (Bella and De Franceschi 1980).

Three days after the 1979 fire, it was sown to a mixture of seed of 2.8 kg ha^{-1} of alfalfa (*Medicago sativa* cv. Drylander) inoculated with rhizobium, and 7 kg ha^{-1} each of bromegrass (*Bromus inermis* cv. Magna), orchard grass (*Dactylis glomerata* cv. Kay), and creeping red fescue (*Festuca rubra* cv. Boreal). The seed was broadcast as evenly as practicable, from a "cyclone" seeder.

The area was subdivided into six paddocks of an average 0.5 ha each, to provide three replications of each of two grazing treatments. Approximately 30% of each paddock was native grassland, and the remainder was regenerating aspen forest. Three paddocks were heavily grazed with cattle from 5th to 17th July (12 days), soon after emergence of suckers of regenerating forest species, this being the time when root carbohydrate concentration is lowest (Schier and Zasada 1973).

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[3] DBH: Trunk diameter at breast height (1.3 m).

The remaining three paddocks were heavily grazed from 22nd August to 1st September (10 days); i.e. just prior to the breakdown of leaf chlorophyll in late summer, and approximately coinciding with the expected time of maximum root carbohydrate concentration.

The objective of the grazing treatments imposed was to completely defoliate all accessible material. Since grazing was considered to be a substitute for a mechanical removal operation, the defoliation was conducted over a short time interval to prevent any grazing of subsequent regrowth. In 1979, complete defoliation within about ten days required 8 animals ha^{-1} for early grazing, and 25 animals ha^{-1} for late grazing, where there was more material to be removed. In 1980 the "early" treatment was grazed with 8 animals ha^{-1} from 31st May to 13th June (13 days), and the "late" treatment with 27 animals ha^{-1} from 15th to 23rd August (8 days).

Grazing achieved complete or near complete defoliation of all species, except snowberry, in both treatments. Generally, cattle were more reluctant to graze forest species early than late (see Chapter V), and had to be retained on the early grazed paddocks for longer to achieve comparable defoliation.

Measurements

Density and height of individual woody species within a grazing treatment were estimated from counts within ten 1 m^{-2} fixed quadrat sites established at random within the old aspen forest in each paddock (30 per grazing treatment). Estimates within each grazing treatment were made at the commencement of that grazing period. Daily height measurements in the fixed quadrats were used for non-destructive estimates of weight and botanical composition during the grazing interval (Chapter II).

Biomass and botanical composition estimates were made coincident with grazing in 1979 and 1980, and on July 7 1981, at predetermined distances and directions from the ten fixed sites in each paddock. All material within these fixed 1 m x 0.5 m quadrats was clipped, sorted into species, dried in a draught oven at ca. 100°C for 24 hours, and weighed.

Statistical analysis

Estimates were subjected to analyses of variance by the method of least squares. Treatment variances for biomass and botanical composition were tested against the variance of replications within treatments, this being the sum of replication and replication X treatment variances. The usual experimental error is the replication X treatment variance, but with only two experimental treatments, it was expedient to accept the penalty of a larger error variance because it allowed more degrees of freedom for testing treatment effects. There was no advantage in expanding the error variance for testing density and height data. Consequently, variances of density and height data were tested against replication X treatment variances.

Effects of grazing season treatments on biomass were analysed separately for each sampling time (May or August 1980, and July 1981). Comparisons between samplings were not made because seasonal sampling time varied. The estimates of biomass were of plants with different seasonal growth patterns. Consequently, comparisons of biomass, determined at different seasonal times, would be confounded with these different growth patterns.

Sampling times for density and height estimates for 1979 and 1980 were established to serve the purposes of a study in cattle diet preferences described in Chapter V. Early grazing treatment estimates were made in June or early July, and the late grazing estimates in late August. Consequently, effects of grazing season, within 1979 or 1980, on density and height of woody plants, could not be compared. Since the seasonal time of sampling in 1979 and 1980 was similar, comparisons of density and height could be made between those years.

In 1981, all treatments were sampled in early July, and comparisons between grazing season treatments were possible. A comparison between density and height for 1979/80, and 1981 was invalid because of differences in season of sampling.

Estimates of the biomass of raspberry in 1979/80, which are based on density and height measurements are subject to the same analysis limitations as density and height estimates.

B. Results

Botanical composition

Since the botanical composition interaction in 1980 between grazing treatments and sampling times was not significant, the two sampling times were combined in Table III.1, which shows the botanical composition of early and late grazing treatments for 1980, determined in May and August 1980. Grazing treatment had a profound effect on botanical composition. While the overall proportion of woody species was constant between treatments, the proportion of aspen was much lower in the late-grazed paddocks, its place being filled by a greater proportion of rose and snowberry.

"Grass" consisted mainly of sown grasses and alfalfa, but included a small proportion of volunteer grass species, especially *Poa pratensis*. Grass contribution was greater in early-grazed than the late-grazed paddocks. There was no significant interaction in botanical composition between grazing time and sampling time which indicated that the botanical composition within the 1980 growing season was not changed significantly either by the growing season, or by the grazing of the early-grazed treatments.

Table III.1. Proportion (%) of total aerial biomass in 1980, of the major components of regenerating forest, for early or late grazing treatments.'

	Grazing season			
	Early		Late	S.E.
Aspen	28.7	**	2.5	5.9
Rose	9.3	*	18.8	5.2
Snowberry	17.0	*	34.6	13.2
Total woody†	55.1		55.9	9.6
Grass‡	27.6	**	18.0	5.6
Other spp.	17.3		26.1	14.7

' Means of May and August samplings.
† Total of aspen, rose, and snowberry.
‡ Includes alfalfa.
** Difference significant (P<0.01).
* Difference significant (P<0.05).

The only significant changes in botanical composition between May and August 1980 was the increase, in both grazing treatments, in the mean proportion of grass, from 16.8% on May 31 to 28.7% on August 26, and a decline in the proportion of rose from 17.1% to 10.8% (P<0.05). The grass increase replaced small non-significant reductions in woody (7.9%) and "other" (4%) species. "Other" included forbs, raspberry and other woody species, mainly willow, and some saskatoon (*Amelanchier alnifolia*).

In 1981, after grazing treatments had been conducted twice, the pattern for the major species remained the same (Table III.2). Data for both 1980 and 1981 are shown also in Figure III.1, for comparison between years. Raspberry (not

Table III.2 Proportion (%) of total aerial biomass of the major components of regenerating forest, for early and late grazing treatments in July 1981.

	Grazing season			
	Early		Late	S.E.
Aspen	33.0	*	2.6	15.4
Rose	9.3		20.1	14.7
Raspberry	3.2		4.6	4.8
Snowberry	15.7		32.5	17.7
Other woody	5.2		0.4	9.7
Total woody	66.5		60.2	16.6
Alfalfa	1.8		0.2	2.2
Orchard g.	12.0		11.5	3.1
Brome g.	8.2		9.4	10.0
All sown spp.	22.1		21.2	10.5
Other grass	3.5		5.4	3.4
Forbs	5.3		8.1	4.7
Vetches	2.5		5.1	4.0
All herbaceous	33.5		39.8	16.6

* Difference significant ($P<0.05$).

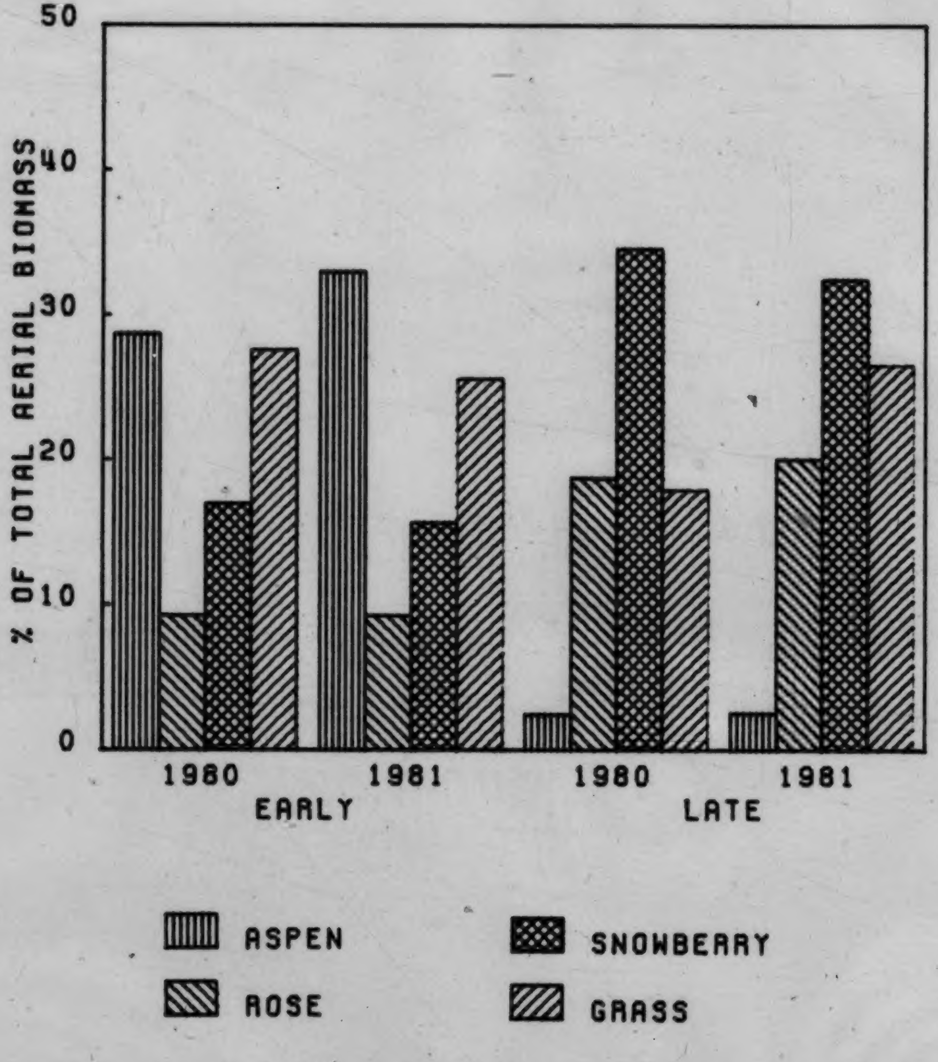

Figure III.1 Proportional contribution (%) of the four major major components of the regenerating forest in early and late grazing treatments in 1980 and 1981.

separated in 1980) made only a minor contribution under both grazing treatments. The greater contribution of "other woody" under early grazing arises from the substantially higher population of willow in replication 1 of that treatment than in the other paddocks. Hence, for "other woody", the effects of replication, and replication X treatment, were highly significant (Appendix A).

The only herbaceous species to be affected significantly by grazing season were alfalfa and vetches, and their responses were opposite, with alfalfa being favoured by early grazing and vetches by late grazing. The contribution of sown species, which was constant in 1981 between grazing season treatments, will be discussed in Chapter IV.

The contribution of "grass" (total of sown species and "other grass", Table III.2) was unchanged for 1980 at 25-27%.

Biomass

Total aerial biomass at the early and late grazing times was not significantly different at any sampling time (Tables III.3, III.4, and III.5). The differences in botanical composition already described, arose from differences in biomass of the individual species. The biomass of aspen in early-grazed paddocks was almost nine times greater than in late-grazed paddocks in May 1980 (Table III.3). By August 1980, it was greater by a factor of 17 (Table III.4) even though the early-grazed treatment had

Table III.3 Yield (kg ha^{-1}) of the components of forest on May 31 1980, for early and and late grazed treatments.

	Grazing season			
	Early		Late	S.E.
Aspen	615	*	70	278
Rose	210		466	276
Snowberry	417		631	501
Total woody†	1242		1167	768
Grass‡	381	*	175	100
Other spp.	366		360	181
Total biomass	1989		1703	703

† Excludes raspberry. ‡ Includes alfalfa.
* Difference significant ($P<0.05$).

Table III.4 Yield (kg ha^{-1}) of the components of forest on August 26 1980, for early and late grazed treatments.

	Grazing season			
	Early		Late	S.E.
Aspen	953	**	56	230
Rose	224	**	605	167
Snowberry	524		1364	1073
Total woody†	1701		2025	1046
Grass‡	1117		791	273
Other spp.	402		1009	757
Total biomass	3220		3824	453

† Excludes raspberry. ‡ Includes alfalfa.
** Difference significant ($P<0.01$).

Table III.5 Yield (kg ha^{-1}) of the components of forest for early and late grazed treatments, sampled on July 7 1981.

	Grazing season		
	Early	Late	S.E.
Aspen	1640 *	136	805
Rose	435	865	785
Raspberry	144	178	186
Snowberry	792	1394	770
Other woody	224	15	398
Total woody	3236	2588	1221
Alfalfa	93	10	128
Orchard g.	561	453	169
Brome g.	377	359	360
All sown spp.	1032	822	395
Other grass	159	209	136
Forbs	231	305	147
Vetches	116	200	167
All herbaceous	1539	1537	507
Total biomass	4775	4125	960

* Difference significant ($P<0.05$).

been grazed in June, while samples from the late-grazed treatment were from exclosures ungrazed in that growing season. In July 1981, the difference was by a factor of 12 (Table III.5).

Generally, biomass trends for species other than aspen were not significant, though, in 1980, they gave rise to significant botanical composition effects. Exceptions were "grass", which was mainly sown species (Table III.3), and rose (Table III.4). Raspberry was not separated from clippings in 1980 because it was considered to make only a minor contribution to overall yield. However, the biomass of raspberry could be estimated from height measurements (Chapter II), and is shown in Table III.6.

Raspberry biomass estimates for early and late grazing treatments in 1979 and 1980 could not be compared because their estimators (height and density) were sampled at different times. Nevertheless, the differences between means are large. No differences between years could be detected in 1979/80. In the early-grazed paddocks, the small plants were totally consumed, and in the late-grazed paddocks, defoliated stems died back. Hence, in both grazing season treatments, raspberry biomass is for new growth sprouting from rhizomes, and one would expect no difference between years other than that due to a decline in vigour of regrowth.

Table III.6. Raspberry biomass (kg ha^{-1}) as estimated from density and height at grazing in early and late grazing treatments in 1979/80, and in July 1981.

	Grazing season	
	Early	Late
1979	83	414
1980	31	321
S.E.	31	106
1981	114	69
S.E.	40	

Plant density and height

The only changes observed within the limits of the sampling schedule were a dramatic decline in the aspen density in late-grazed paddocks from 1979 to 1980, with a very large difference in density between early and late-grazed paddocks apparent in July 1981 (Table III.7).

Height estimates for the four major species are shown in Table III.8. The height of all species, except aspen, declined under late grazing. For raspberry, this reflects declining vigour of regrowth, as stems died back after grazing, and plants resprouted from underground stolons. For rose and snowberry, since their biomass was greater under late grazing (Table III.3), the decreased height suggests increased lateral growth, instead of vertical growth, following grazing. Field observations confirmed this deduction.

Table III.7 Woody plant density (plants m^{-2}) for early (E) and late (L) grazed treatments at grazing in 1979 and 1980, and in July 1981.

	Aspen		Rose		Raspberry		Snowberry	
Year	E	L	E	L	E	L	E	L
1979	18.3	12.6	9.4	18.0	13.1	17.7	21.6	31.2
		**						
1980	20.3	1.3	14.6	14.4	11.2	14.9	28.2	23.1
S.E.†	5.6	1.2	5.3	3.3	5.0	3.6	5.3	5.7
1981	12.9	** 0.9	23.4	26.0	19.0	26.1	36.1	46.9
S.E.†	3.3		14.8		11.6		34.4	

** Difference significant ($P<0.01$).

† S.E. Standard errors, between years in 1979/80, and between grazing treatments in 1981.

Table III.8 Woody plant height (cm) for early (E) and late (L) grazed treatments at grazing in 1979 and 1980, and in July 1981.

	Aspen		Rose		Raspberry		Snowberry	
Year	E	L	E	L	E	L	E	L
1979	21.9	71.1	20.7	51.3	19.9	50.6	24.3	45.5
				*		*		**
1980	34.9	63.5	17.6	48.1	12.8	35.0	24.1	37.3
S.E.†	19.9	14.5	3.4	1.9	7.5	7.6	7.9	3.5
1981	51.6	55.5	24.8	28.9	17.6	14.7	28.1	31.6
S.E.†	13.1		5.6		5.0		11.4	

* Difference significant ($P<0.05$).

** Difference significant ($P<0.01$).

† S.E. Standard errors, between years in 1979/80, and between grazing treatments in 1981.

C. Discussion

Two quite different plant communities developed under the two grazing treatments. With early grazing, the major species within the old forest were grasses and aspen suckers, the latter appearing in clumps, mostly at the base of old burnt trees. Snowberry was also a significant component. With late grazing, the major species were rose, snowberry, and grasses, with little or no aspen.

This dramatic effect of late grazing on aspen regeneration was established after only one heavy grazing (Tables III.1 and III.3). The greater proportion of rose and snowberry under late grazing, was established by May 1980 also (Table III.1), but the effects were no longer significant in 1981. In 1981, the test of significance was much more stringent, because there was only one sampling, with consequently fewer degrees of freedom for error variance. The means are consistent with previously established trends. The proportion of grass was greater in early-grazed than late-grazed paddocks in 1980, but not in 1981, and this interaction will be discussed in the next chapter. Clearly the timing of defoliation is critical for plant succession in a regenerating forest, and affects different species in different ways.

The initial suppression of rose and snowberry by early grazing is consistent with previous studies on time of clipping of range shrubs. Willard and McKell (1978) found the same relative effects of June 1 and September 1 clippings on little rabbitbush (*Chrysothamnus visidiflorus*) and a palatable species of snowberry, (*Symphoricarpos vaccinioides*) in Utah. Wright (1970) observed a similar depression in regrowth of two species of *Artemisia* from clipping in June or July relative to August or September.

Early grazing in 1979 may have terminated growth in rose and snowberry before they had a chance to replenish carbohydrates depleted in the spring after burning. Regrowth of snowberry after grazing did not commence until the following spring. With late grazing, both shrubs had a full growing season to recover their carbohydrate levels after burning. Willard (1972) reported that root carbohydrates in rabbitbrush in the spring following a June clipping were lower than from later clippings. He detected no such difference in the roots of snowberry (*S. vaccinioides*). Regrowth measurements may be a more sensitive estimate of a plant's energy status than TNC analysis. Alternatively, the smaller regrowth of snowberry following early grazing in this experiment may arise from the effect of defoliation on one of the unknown factors, perhaps hormonal, to which Willard (1972) referred.

The only species which increased in height after grazing was aspen (Table III.8). The decapitation of actively growing stems of aspen was shown by Maini (1966) to accelerate height growth from lateral buds. Neither height nor biomass data show any evidence of a decline in vigour of aspen after two years of heavy early grazing.

The reason for the suppression of aspen suckering by late grazing is not clear. In the most comprehensive study of top removal yet reported (Berry and Stiell 1978), all top growth was removed annually after leaf fall. The biomass of aspen, prior to cutting in the following autumn, was actually increased in the first two years of treatment. In the study by Smith *et al.* (1972) cattle grazed an average of 25% of suckers in July and, after 4 years, had reduced sucker number by 50%. There are no other reports of control operations on aspen being carried out in the last half of the growing season. Of interest is a report by Van Nickerk *et al.* (1978) in which herbicides gave best control of *Acacia* species in southern Africa, when applied in late summer after foliage expansion was complete.

Aspen sucker growth has been related to root carbohydrate concentration (Tew 1970, Schier and Zasada 1973), which may be depleted by repeated removal of tops (Schier 1976). Since root carbohydrate is lowest in spring (Schier and Zasada 1973), a decline in the vigour of regrowth would seem to be most likely from defoliation in spring, particularly if regrowth is most active at that time. This is the experience with other shrubs (Willard and McKell 1978, Wright 1970). Also Trlica *et al.* (1977) found that rabbitbrush recovered its carbohydrate reserves in 14-16 months after cutting at all phenological stages except during the period of rapid growth. They found that defoliation at the time of lowest carbohydrate concentration reduced regrowth, and subsequent carbohydrate levels, more than at any other time. Consequently, it seems unlikely that late-grazed aspen plants suffered carbohydrate exhaustion after one defoliation, when plants grazed early, at the time of lowest carbohydrate, resuckered vigorously.

A change in auxin:cytokinin relationships to suppress suckering from August defoliation seems an unlikely explanation because, even if initiation was inhibited, perhaps by a cessation of root tip activity and a consequent lowering of cytokinin concentration (Skene 1975), there are abundant suppressed primordia present on the roots of most clones at all times (Schier 1973a). Existing primordia would remain quite viable, but this was not the case here where no further suckers emerged.

Some other factor is involved, apparently as a result of grazing prior to leaf senescence. Zehngraff (1946) suggested that suckers released by spring logging and emerging in mid-summer are not thoroughly "hardened off" by fall and consequently may be winter-killed. If suckers were released by a defoliation in August and emerged before conditions became too cold for growth then probably they would freeze. Perhaps, in this way, existing viable primordia would be eliminated, leaving no primordia to produce suckers the following spring. Temperatures which were low enough to kill very young shoot outgrowths, might prevent the formation of new primordia at that time. This might explain the failure of aspen to re-sucker, provided the existing defoliated stems also perished, as indeed they did after late grazing, though not after early grazing.

A possible explanation for the killing of existing suckers by late August defoliation is by dormancy inhibition. Abscisic acid (ABA) is synthesised in chloroplasts in the leaves (Zeevaart 1977) and transported out of the leaves to the stem and apex (Phillips *et al.* 1980), where it has been associated with the development of bud scales and other characteristics of winter dormancy in blackcurrant, beech (Wright 1975), birch (Harrison and Saunders 1975) and willow (Alvim *et al.* 1976). Other hormones, specifically gibberellins and cytokinins, also have an interactive role. However, ABA appears to be the main growth terminator, its action being prevented or "antagonised" by the presence of gibberellins or cytokinins (Alvim *et al.* 1976, Thomas *et al.* 1965). Alvim *et al.* (1976) found levels of ABA in the xylem sap of willow to be high after the shortening of days begins in late June and to remain fairly high till the end of August. Thus, movement of ABA out of the leaves and into apical and lateral buds occurs continuously after ABA synthesis has been stimulated, and gibberellin levels reduced by a shortening of day length (Wareing and Saunders 1971).

Eliasson (1969) established that an inhibitor, which is associated with the formation of resting buds, occurs in *Populus tremula*. He found that leaves in August contained only low concentrations of inhibitor and suggested that this was a result of export to stems.

If, as seems likely, these reactions occur in *Populus tremuloides*, then, removal of leaves in August might remove the source of ABA, thereby preventing the normal development of dormancy. Plants left in a non-dormant state would freeze in the winter.

Further support for this hypothesis was provided by Cozens and Wilkinson (1966) who found that decapitation of blackcurrant stimulated breaking of dormancy in the top two or three buds on the decapitated stem. Total defoliation, however, released buds over the whole plant. They claim that the source of inhibition of buds in late summer and early autumn was removed by removal of leaves.

It is possible that the establishment of winter hardiness in the roots was also upset by the August defoliation. The argument is less tenable however, because Phillips *et al.* (1980) found ABA levels in the roots of maple under short days to be very low and that ABA from leaves was transported acropetally. Cohen *et al.* (1978) also recorded ABA levels in maple roots during the establishment of dormancy to be lower than levels recorded in the xylem sap of willow (Alvim *et al.* 1976) by a factor of 10^{-6}. This low concentration may very well be synthesised in the root tips (Audus 1975), or perhaps, released from a bound form, and would not be reduced by the cessation of the flow of ABA from the leaves. Pilet and Elliott (1981) provided supporting evidence of ABA synthesis in root tips, and basipetal transport in roots of *Phaseolus vulgaris*.

Obviously, there is room for further investigation into the cause of this most interesting effect of August defoliation.

IV. ESTABLISHMENT OF FORAGES

A. Introduction

After mechanical clearing of aspen forest, successful germination and initial growth of forage seedlings may be achieved by sowing with a drill (Bailey 1972). If herbicides or fire have been used to remove the overstory, logs and stumps prevent the placement of seed through a drill, and broadcasting may be the only feasible method of sowing. Very much poorer establishment can be expected from broadcasting compared with drilling (Nelson *et al.* 1970), but in some circumstances sufficient success has been achieved to make the procedure worthwhile (Campbell 1968, Cullen 1970).

Plant competition severely reduces the growth of seedling grasses. Bryan and McMurphy (1968) improved the yield of sown grass swards by removal of weeds, primarily crabgrass (*Digitaria sanguinalis*). Cullen (1970) improved establishment of orchard grass and ryegrass (*Lolium perenne*) by controlling competition by close grazing and/or use of a pre-sowing herbicide. Following establishment by broadcasting, the suppression of competition from regenerating brush species was investigated by imposing heavy grazing with cattle early or late in the growing season.

B. Methods

Experimental design

The experiment was conducted at the University of Alberta Ranch, Kinsella Alberta. The layout, establishment procedure, and grazing treatments were described in detail in the previous chapter.

Measurements

Ten 1 m^2 quadrat sites per paddock were established randomly within the aspen forest community. Their position was fixed. Seedlings of sown species were obscured by shrub regrowth prior to grazing. Hence, the seedlings within the fixed quadrats in each grazing treatment were counted at the conclusion of grazing in that treatment. Counts were conducted for alfalfa only in 1979, and for all sown species in 1980. and in July 1981.

In 1980, yield of sown species was estimated on May 31 and August 26 by harvesting all plant material within 0.5 m^2 quadrats (10 per paddock, 30 per grazing treatment) situated 2 m from the fixed quadrats in a previously assigned direction. Plants harvested in August had been protected during grazing by an exclosure. All harvested material was sorted into sown species and other, and was then dried and weighed. On July 7 1981, the plant material at the fixed sites was harvested, sorted, dried, and weighed, in the same way as in 1980. Grazing effects on density, and yield estimations, were subjected to least squares analysis of variance, using the variance of treatments within replication for estimation of error.

To provide an ungrazed comparison, areas of forest adjacent to the experimental paddocks were burned and sown to forage species in an identical manner to the area within the experimental boundary. Estimations of grass and alfalfa yield are presented for comparison. As ungrazed areas were not randomised with treatments, they were not included in the analysis.

C. Results

Rainfall

After sowing there were 15 days of dry weather. In the following 22 days there were 19 wet days during which rainfall totalled 42 mm. Monthly rainfall for May and June was below average (6% and 60% of the 18 year average respectively), but the number of wet days for June (20 days) was almost double the average. Exceptionally good rains fell in July (120 mm). Rainfall for the whole growing season was 20% below average in 1979 (259 mm) and 57% above average in 1980 (508 mm).

Plant yield and density

Yields of sown species, and their contribution to total plant biomass in spring and late summer 1980, were consistently higher in the early-grazed treatment (Table IV.1). Their relative contribution to total biomass increased through the 1980 growing season in both treatments (P<.05). Yield of sown species in ungrazed areas was 10 kg

Table IV.1 Yield (kg ha^{-1}) and contribution to total biomass (%) of sown species, for early- and late-grazed treatments on May 31, and August 26 1980, and July 7 1981.

		Grazing season			
Sample time		Early		Late	S.E.
May 1980	Yield	381	*	175	100
	%	20.4	*	13.3	3.9
Aug 1980	Yield	1117		791	273
	%	34.7	*	22.6	3.9
July 1981	Yield	1032		822	395
	%	22.1		21.2	10.5

* Significant (P<.05).

Table IV.2 Yield (kg ha^{-1}) and contribution to total biomass (%) of alfalfa and grasses, for early- and late-grazed treatments on July 7 1981.

		Grazing season		
Species		Early	Late	S.E.
Alfalfa	Yield	93	10	128
	%	1.8	0.2	2.2
Orchard grass	Yield	561	453	169
	%	12.0	11.5	3.1
Brome grass	Yield	377	359	360
	%	8.2	9.4	10.0
Other grass	Yield	159	209	136
	%	3.5	5.4	3.4

* Significant (P<.05).

ha^{-1} or 0.3% of total aerial biomass.

By July 1981, the proportion of sown species had begun to decline under early grazing, and was no longer different from the proportion under late grazing (Table IV.1). Individual grasses showed no differences in yield between grazing treatments (Table IV.2).

The density of alfalfa was consistently greater under early than late grazing (Table IV.3). Brome grass responded similarly in 1980, but the difference had disappeared by 1981. Creeping red fescue was no longer present to a measurable degree in 1981.

D. Discussion

Establishment of forages by broadcasting into the ash following burning was successful in a year in which sowing preceded 3 weeks of almost continuously wet weather, and a season of generally good moisture conditions. Dry matter yields of over 1000 kg ha^{-1} were obtained from an area that probably was yielding 10-20% of that amount (Table I.1), prior to commencement of brush control operations.

Nelson *et al.* (1970) broadcast seeds of *Agropyron* spp. in Washington, where annual rainfall was only 330 mm. They found that surface-sown seeds were highly vulnerable to a period of drying weather after initial imbibition. No spring-broadcast seeds germinated in their conditions. Likewise, McWilliam and Dowling (1970) reported that as water potential decreased (i.e., increasing drought),

Table IV.3. Density (plants m^{-2}) of alfalfa and sown grasses at completion of early or late grazing in 1979/80.

		Grazing season			
Species	Year	Early		Late	S.E.
Alfalfa	1979	16.8	*	8.6	3.8
	1980	11.4	**	0.5	3.8
	1981	15.5	*	2.8	4.1
Orchard grass	1980	25.0		16.8	15.2
	1981	24.5		22.4	9.0
Brome grass	1980	23.7	*	2.7	10.0
	1981†	56.3		71.6	69.0
C.R.Fescue	1980	10.5		2.9	7.0

* Significant ($P<.05$), ** Significant ($P<.01$).
† Stems m^{-2}

% germination of pasture seeds declined. Their results highlighted the variation in the ability of different species to germinate in dry conditions.

Hence, the success of any system of broadcasting will depend on the maintenance of moist soil in contact with the seed, either through the fortuitous continuation of wet or overcast weather, or the equally fortuitous falling of seed into cracks or depressions, there to be covered by washed soil (or ash). The high seeding rates used here increased the chance of seeds falling into a favourable micro-environment. The chances of favourable weather conditions occurring in the aspen parkland are much greater than those experienced by Nelson *et al.* (1970) who conducted their work in a region of considerably lower rainfall. The choice of species which are able to germinate under conditions of low water potential will increase the chance of a successful establishment (McWilliam and Dowling 1970).

Keller *et al*. (1970) suggested that germination after sowing can be accelerated by soaking seeds for 60 hours prior to broadcasting. McWilliam and Dowling (1970) improved the rate of imbibition and % germination by coating seeds with lime. These techniques are likely to be applicable to post-burning establishment.

Campbell and Swain (1973) achieved better seedling germination and survival when seeds were dropped into dead plant residue. Absence of such residue would appear to be a disadvantage for seedling establishment following burning.

This experiment confirms the importance for seedling survival and growth, of removing competition early in the life of the seedling. Establishment and growth of seedlings was negligible in the absence of grazing. Heavy grazing early in the growing season was much more effective for establishment of forages than grazing towards the end of the growing season. Similarly, Cullen (1970), and Campbell and Swain (1973) reported enhanced seedling establishment after plant competition was reduced by grazing.

Evidently any damage to young seedlings from trampling shortly after emergence was offset by the advantages of reduced competition from shrubs. At this early stage, seedlings were too small to be damaged directly by grazing. Similarly, Love (1944) found that spring grazing with sheep did no damage to newly-emerged ryegrass (*Lolium perenne*) seedlings. Campbell and Swain (1973) pointed out that, although grazing may eliminate some established plants, losses of seedlings incurred by not grazing could be greater.

In the third growing season after sowing, the effects of competition with shrubs began to alter the pattern established in the first two years when shrubs were small. In the late-grazed paddocks, yield of sown species, and their contribution to total biomass was unchanged between 1980 and 1981 (Table IV.1). In the early-grazed paddocks, grass yield remained constant, but the biomass of woody plants increased (Tables III.2 and III.3). The woody plants were successfully competing against the grass component in the early-grazed treatment. The major woody species difference between the treatments was the difference in the aspen component. This suggests that it was aspen that was successfully competing against grass.

The decline of alfalfa density from 1979 to 1980 can be attributed to inappropriate management for the species. Alfalfa is very intolerant to any competition, especially in the seedling stage (Christian 1977). Under more appropriate management (hay cutting or rotational grazing to reduce the competitiveness of associated grasses), the decline might have been avoided.

Cattle may be reluctant to graze shrubs in some conditions. In the early grazing of 1980, shrubs were not browsed until most of the graminaceous material had been consumed. For early grazing of a one year old stand of shrubs and grasses, animals would need to be held sufficiently long, and in sufficient numbers, to consume both the palatable grasses and the less preferred shrubs. Under range conditions, some method of concentrating the cattle on regenerating shrubs, such as temporary electric fencing, may be necessary for early-season suppression of shrubs.

V. GRAZING PREFERENCES OF CATTLE IN REGENERATING ASPEN FOREST

A. Introduction

Relatively large quantities of browse regenerate in aspen forest following burning or clear cutting (Sampson 1919, Bailey 1972, Berry 1973, Perala 1979). In fact, burning of aspen forest is a recognised practice for improving the availability of winter browse for wild ungulates (Byelich *et al.* 1972, Kayll 1974, Patton and Jones 1977). Aspen is an important source of browse for deer, elk and moose (Krebill 1972, Smith *et al.*1972, Mueggler and Bartos 1977, Penner 1978, Parker and Morton 1978). In some situations (Smith *et al.* 1972, Bartos and Mueggler 1979) browsing by ungulates may be heavy enough to threaten aspen stand survival.

Although specifically adapted to grass forages, sheep and cattle also use aspen suckers under some circumstances. Smith *et al.* (1972) recorded the grazing of 18.3% of available aspen sprouts by cattle in the first year after clear cutting in Utah, but only 3-4% in the next two years. In Alberta, three years after herbicide treatment, Hilton and Bailey (1974) found that cattle with access to both grassland and regenerating forest, from late-June to mid-August, consumed from 3 to 43% by weight of total available dry matter of aspen suckers. The level of available alternative forages, and the ontogenetic stage of all species present, is likely to have a major influence on diets (Heady 1964). Rosiere *et al.* (1975a) found that the diets of cattle on open grassland depended, partly, on the relative availability of various sward components. Gammon (1978) showed how the relative preference for various sward components changes through the year.

Since these factors may influence the propensity of cattle to browse in a regenerating aspen forest, an experiment was conducted to determine the relative selection by cattle of the major components of a regenerating aspen forest seeded to forages, and the adjacent grassland, as influenced by:

1. season of grazing
2. stand age
3. the changing availability of component species.

B. Methods

Experimental design

Observations on diet selection were performed in the experiment described in Chapter III, in which cattle grazed burned and seeded aspen forest early or late in the growing season in 1979 and 1980. They were retained in the experimental paddocks until all edible material had been consumed or trampled, in order to determine how their apparent preference responded to sequential depletion of the various plant components.

Grazing times were:

1979	Early	July 5 to 17.	(12 days)
	Late	August 22 to September 1.	(10 days)
1980	Early	May 31 to June 13.	(13 days)
	Late	August 15 to 23.	(8 days)

The early grazings took place when sufficient plant material had emerged to support the smallest practical herd (three animals) for ten days. Actual yield at commencement was 1700 kg ha^{-1} in 1979 and 1800 kg ha^{-1} in 1980. The late grazings took place after elongation of aspen stems had ceased but before leaves showed any yellowing, prior to senescence.

Measurements

Yield in the grassland was estimated prior to grazing and daily through the grazing period from the weight of plant material clipped from six 0.5 m^2 frames randomly placed in the grassland community in each paddock. Forest biomass was estimated prior to grazing and at irregular intervals through the grazing period, to estimate the rate of removal of brush in relation to rate of removal of grass in the grassland community. Estimates were derived from clips of all plant material within randomly placed 0.5 m^2 quadrats, ten per paddock.

To observe the differential removal of individual species, ten fixed 1 m^2 observation sites were established randomly within the aspen forest in each paddock. The height and number of each species was measured prior to grazing and daily through the grazing periods, except that observations were taken over only 10 days in the early grazing of 1979, and 12 days in early grazing 1980. An estimate of growth during the grazing period was determined from ten 0.5 m^2 clips taken at the end of the grazing period from within exclosures placed in the vicinity of the fixed observation sites. Growth was taken as yield within exclosures at the termination of grazing less yield at commencement.

The experimental paddocks were subjected to considerable plant damage from trampling. In the measurements of height and density, if a trampled plant was still attached to its base, though prostrate, it was considered to be a live plant, and its stem length measured. If a plant was dead, it was not included in the estimates.

During the grazing period in 1979, samples of the four major woody species in the regenerating forest were collected and used to establish a relationship between plant height, entire or browsed, and plant weight, by the procedure described in Chapter II. The process was repeated in 1980, for early-grazed aspen.

The relationship between biomass and days of grazing, for each of the four species, was analysed by least squares regression, using days-grazing as a covariate, and testing the slopes of the regression of weight on days-grazing by comparing the variance for the combined covariate/factor interactions with the error variance. The regression analysis was based on plot means determined on each day during the grazing period. The regression coefficients for the four covariate/factor interactions represented the slopes of the four curves of linear decline in biomass of the four species. Differences in slope were tested using the standard errors of these coefficients (Neter and Wasserman 1974 p.166). Means adjusted to the covariate value of zero represented the intercepts, and are the estimate of biomass before grazing.

Palatability Index

Silen and Dimock (1978) developed a model describing the relationship between plant palatability and availability. This model was used to develop a diet palatability index based on the changing level of availability of individual species through the grazing period.

The model employed a palatibility index (P), which encompassed the factors affecting an animal's response to a given species, if availability of all species were equal. It also required an availability index (A), which was calculated as the biomass of a given species, expressed as a percentage of total biomass. As adapted here, plant consumption (E) was a function of the product of the availability and palatability for a given plant type expressed as a proportion of the product of the availability and palatability for all plant types, multiplied by the total plant biomass (W):

$$E_{(i)} = \frac{A_i \times P_i}{\sum_{i=1}^{n} A \times P} \times W_{(i-1)}$$

where E(i) is consumption of a given species on the ith day, and W(i-1) is the total plant biomass at the beginning of that day. The palatability index was calculated for each day of grazing using an iterative computer programme shown in Appendix C.

The same analysis used for plant biomass was used to analyse relative change in palatability over the grazing period, the relative palatability of plants on offer in an ungrazed forest, and their mean relative palatability over the grazing period. For the latter, the palatability index means adjusted to the covariate (days-grazing) mean were compared among species.

C. Results

The botanical composition of the regenerating forest in 1979, as estimated from height and density data, and botanical composition in 1980, is presented in Table V.1. In the early-grazed paddocks from 1979 to 1980, the proportion of raspberry and snowberry declined, while, in the late-grazed paddocks, aspen declined and snowberry increased. Sown grasses became established in both treatments.

Table V.1. Botanical composition (%) of regenerating aspen forest in early and late grazed paddocks, estimated prior to grazing in 1979 and 1980.

	1979†		1980	
	Early	Late	Early	Late
Aspen	23	36	29	2
Rose	10	25	9	19
Raspberry	17	14	2†	10†
Snowberry	44	24	17	35
Grass			28	18
Other	6	1	15	16
Total biomass kg ha^{-1}	1700	4000	2000	3800

† Estimated from density and height data.

Selection: grassland versus forest

The declining biomass of regenerating forest and adjacent grassland during grazing in 1979 and 1980, is shown in Figures V.1 and V.2. In the early-grazing treatments, the cattle deferred browsing in regenerating forest until the adjacent grassland yield had been reduced to 750 kg ha^{-1}. In the late-grazing treatment, the forest was grazed from commencement, and extensive browsing occurred when the grassland still yielded almost 2000 kg ha^{-1}.

In 1980, a similar pattern of grassland and shrub removal was evident in the late grazing (Figure V.2), but in the early grazing, the pattern, at first glance, appeared to have changed. Consumption of 'forest' species up to day 4

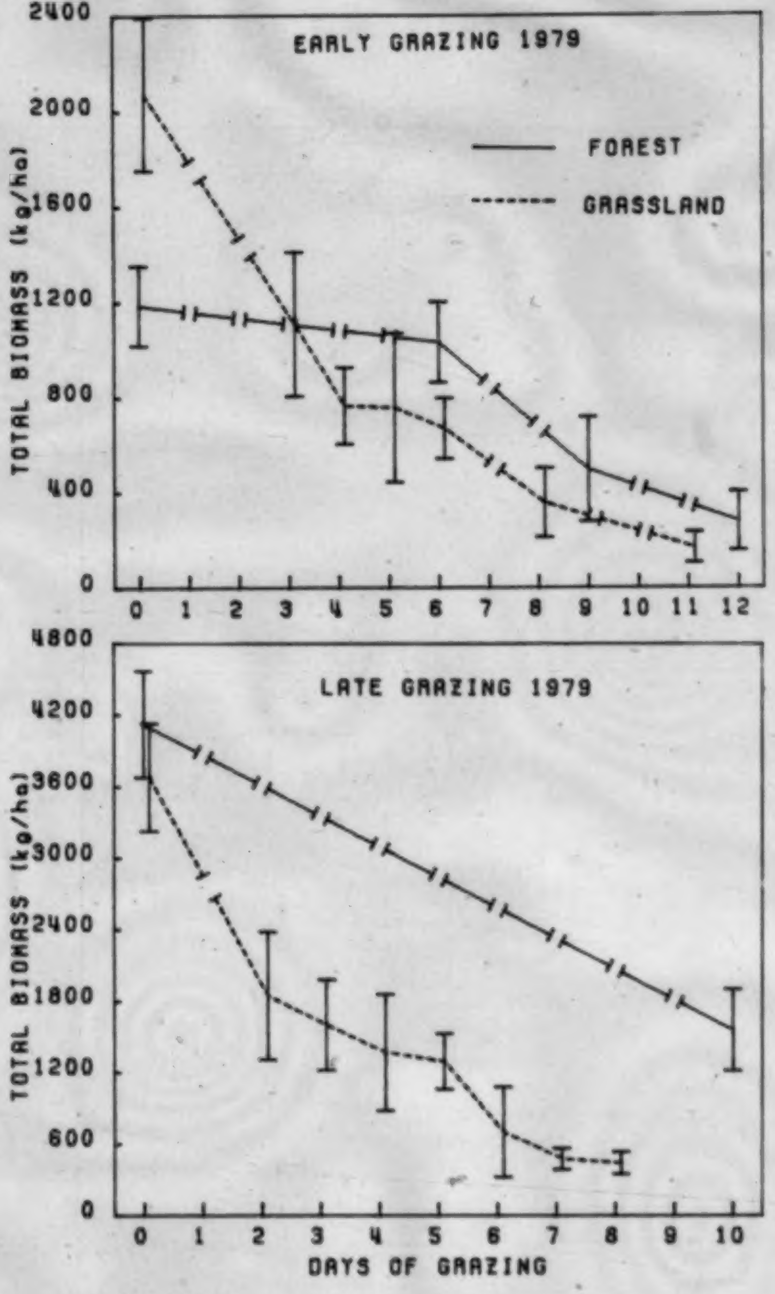

Figure V.1 Biomass of grassland and forest (kg ha⁻¹) during early and late grazing in 1979, showing 95% confidence intervals. In late-grazed forest, only pre- and post-grazing estimates were made.

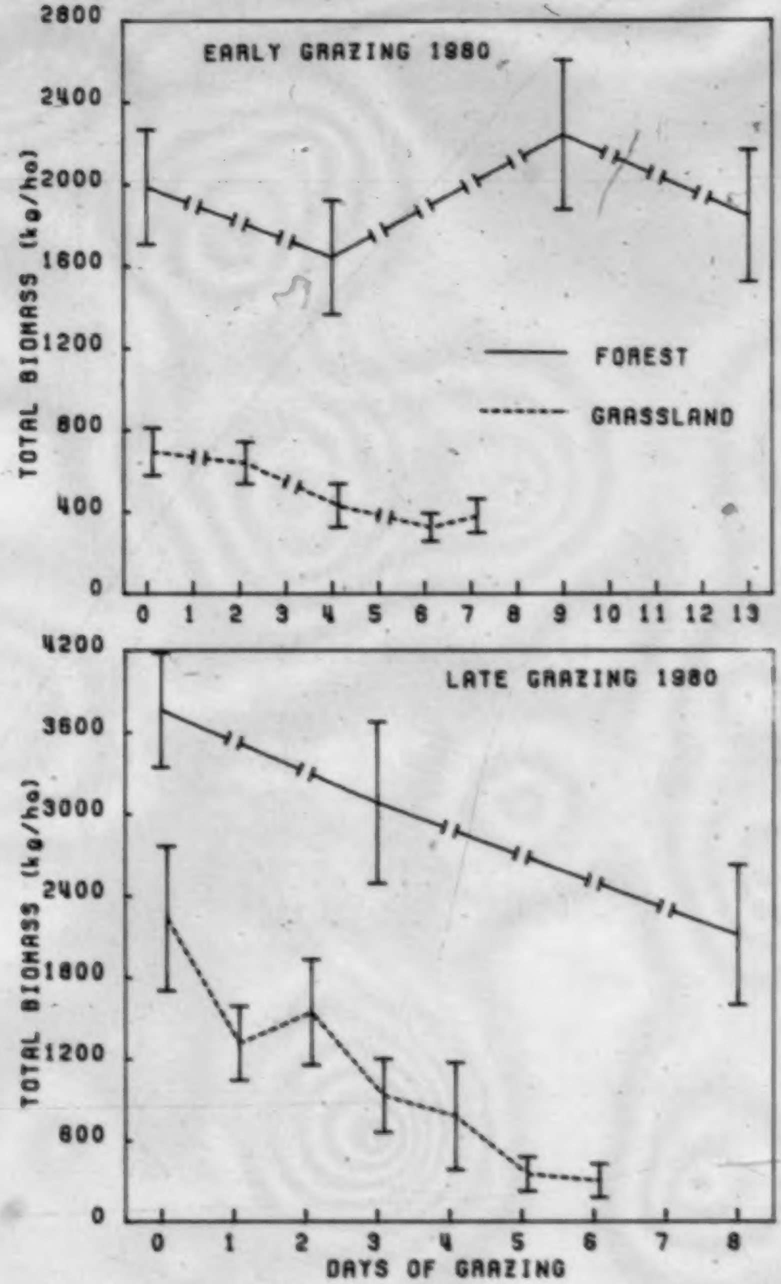

Figure V.2 Biomass of grassland and forest (kg ha^{-1}) during early and late grazing in 1980, showing 95% confidence intervals.

was more rapid than consumption of grassland species. The reason is that sown species, mainly orchard grass, now made up 28% of available forage in the 'forest' community (Table V.1), and animals grazed these preferentially. In Figure V.2, the drop in available 'forest' species up to day 4 arose from the grazing of orchard grass in the regenerating forest. After day 4, the cattle apparently preferred grassland, and had reduced it to a minimum plateau level of about 300 kg ha^{-1} by day 7.

Dry weather prevailed in May. On days 3,4 and 5 of the grazing period it rained. During the wet weather the animals appeared to graze less, and to preferentially graze the grassland community (Figure V.2). The effect of relief from drought, on woody plants (as yet unbrowsed), produced an increase (non-significant) in available 'forest' species from day 4 to day 9 (Figure V.2).

Selection within regenerating forest

Figures V.3, V.4, V.5, and V.6 show the decline in aerial biomass of the four major shrub species in the regenerating forest, for each of the four grazing periods. Intercepts and linear regression coefficients for species biomass on days-grazing are shown in Table V.2. Intercepts are estimates of species yield at commencement of grazing. The slopes are expressions of the average rates of consumption of each species over the whole grazing period. Analysis of covariance for each grazing period indicated that a significant amount of variation in the relationship

Table V.2 Intercepts, regression coefficients, and standard errors for linear regressions of species biomass on days grazing, for four species measured early or late in 1979 and 1980.

Grazing period	Spp.	Intercept (*a*)	Slope (*b*)	r^2
1979 Early	Aspen	130.1 b	-11.1 a	.33
	Rose	44.1 d	-4.3 c	.53
	Raspberry	81.4 c	-7.5 b	.35
	Snowberry	189.4 a	-2.1 c	.00
Std. Error		7.15	1.05	
1979 Late	Aspen	1079.9 a	-24.9 b	.16
	Rose	765.5 c	-12.1 c	.01
	Raspberry	432.2 d	-21.8 b	.52
	Snowberry	825.7 b	-44.1 a	.39
Std. Error		14.6	2.16	
1980 Early	Aspen	487.5 a	-16.7 a	.06
	Rose	19.2 c	-1.3 b	.16
	Raspberry	31.6 c	-2.6 b	.27
	Snowberry	286.1 b	-2.5 b	.00
Std. Error		7.1	0.89	
1980 Late	Aspen	53.7 d	-5.6 c	.05
	Rose	557.8 b	-4.5 c	.00
	Raspberry	352.3 c	-17.3 b	.06
	Snowberry	489.6 a	-28.8 a	.36
Std. Error		13.5	2.38	

a or *b* values within a sampling time followed by the same letter are not significantly different ($P<0.05$).

r^2 significant if greater than 0.12 ($P<0.05$, 30 df).

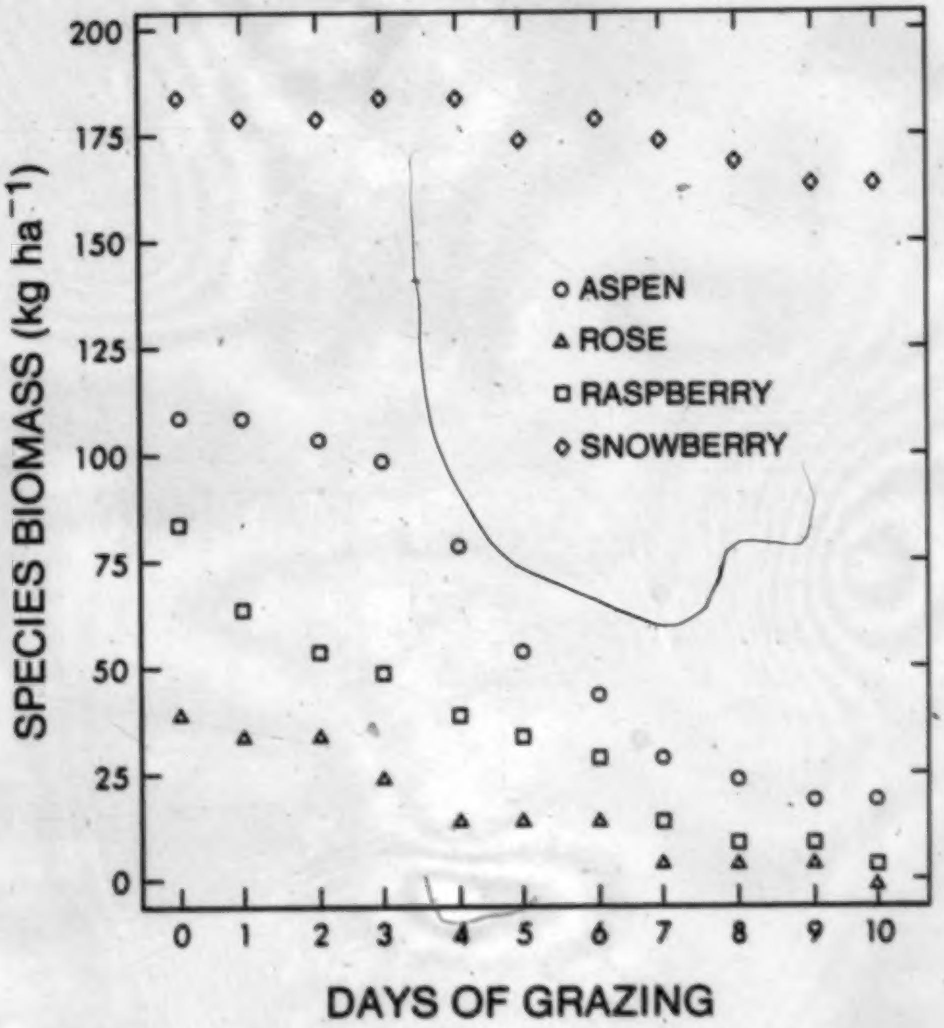

Figure V.3 Biomass of aspen, rose, raspberry, and snowberry during the grazing period, Early 1979.

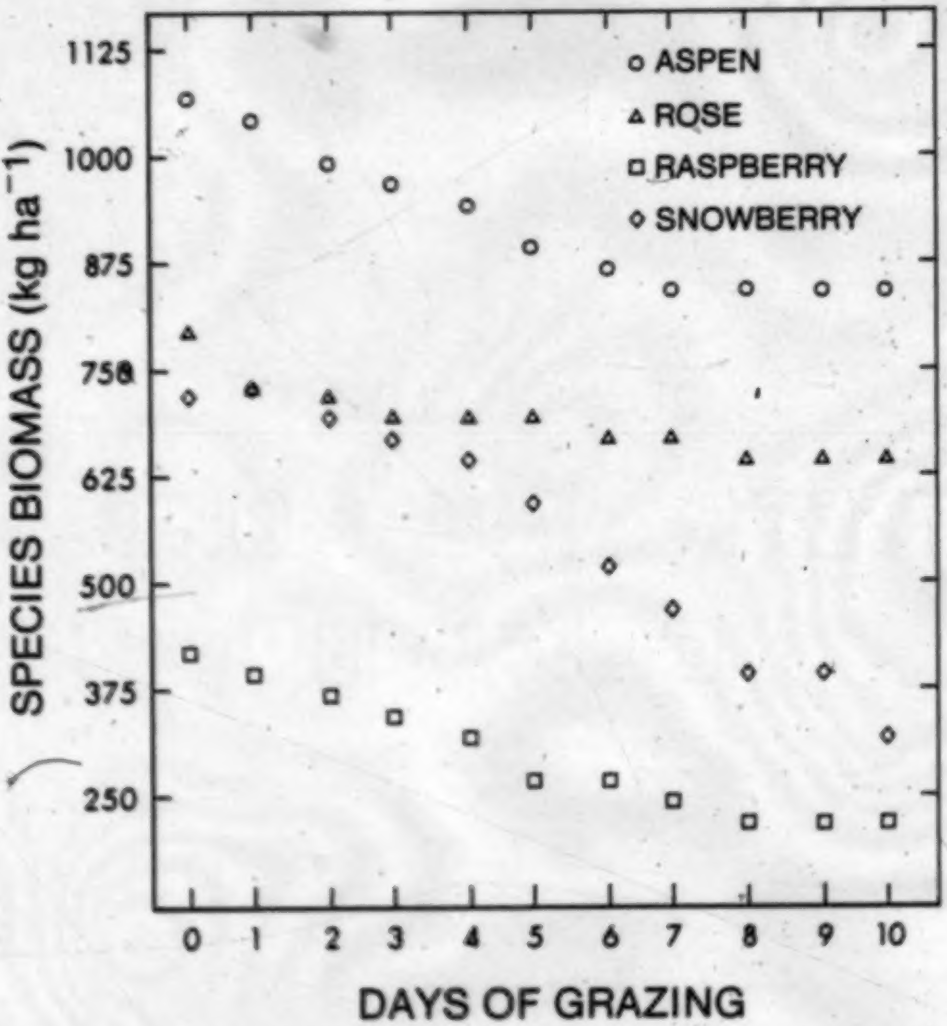

Figure V.4 Biomass of aspen, rose, raspberry, and snowberry during the grazing period, Late 1979.

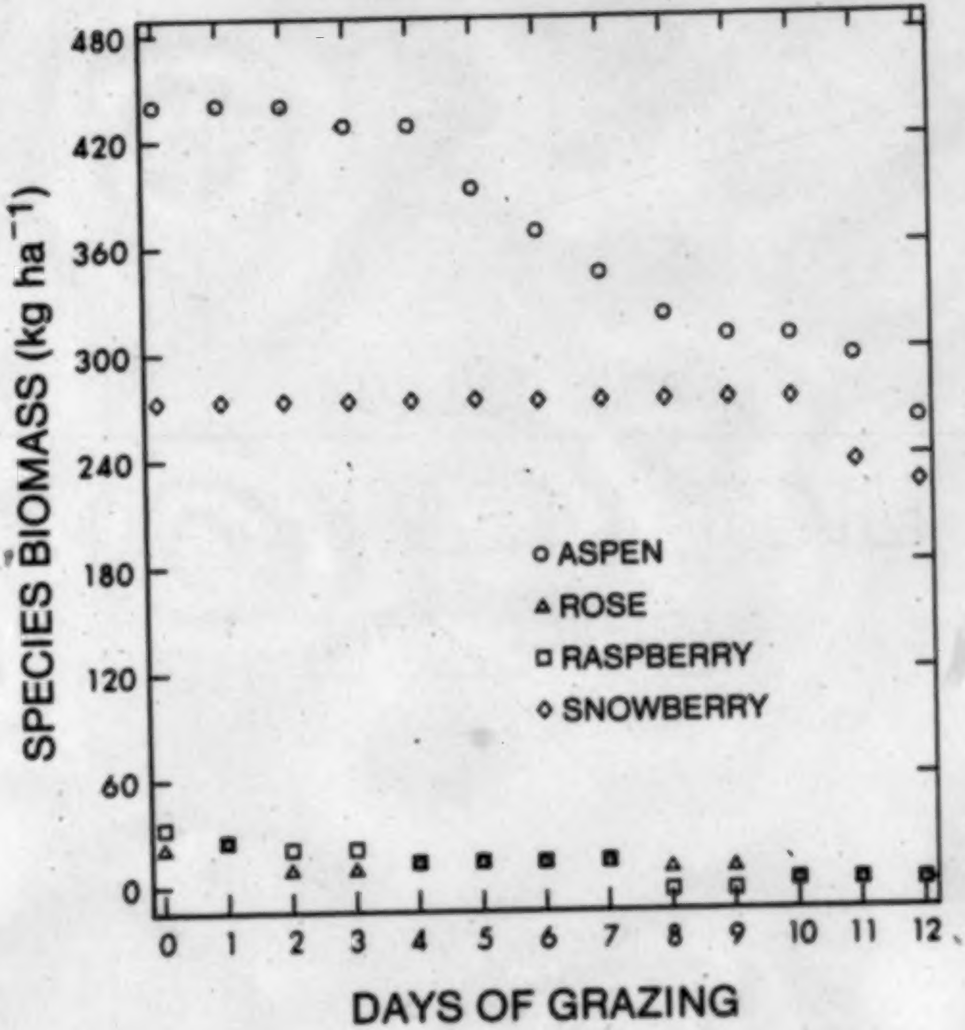

Figure V.5 Biomass of aspen, rose, raspberry, and snowberry during the grazing period, Early 1980.

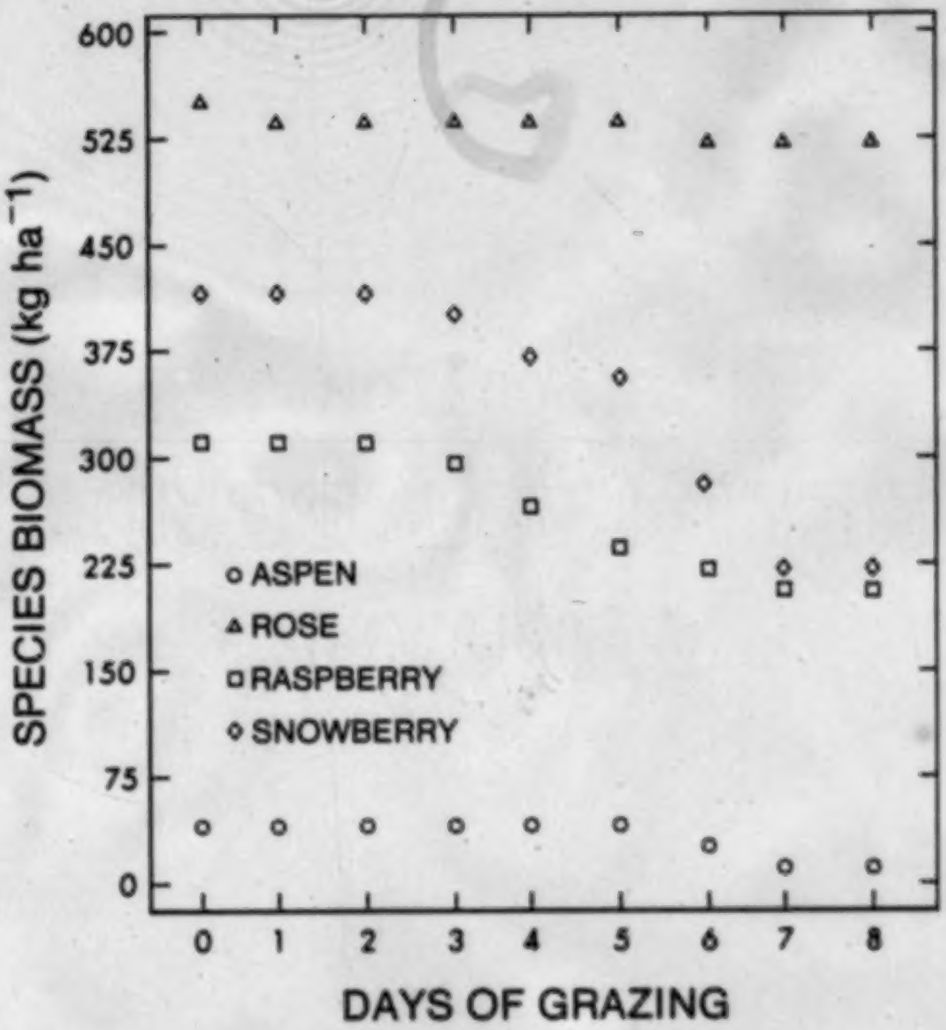

Figure V.6 Biomass of aspen, rose, raspberry, and snowberry during the grazing period, Late 1980.

of biomass with days was explained by the combined interactions between covariate and species (Appendix D). This indicated that the linear slopes of the four species by days-grazing were significantly different from one another at each grazing period.

This analysis does not indicate at what stage in the grazing period consumption took place. For example, in the early 1979 treatment, aspen had a steeper slope than raspberry, but it also had more material initially available. Raspberry was consumed rapidly in the first few days, while the grazing of aspen was delayed until day 4 or 5 (Figure V.3). However, an attempt to show significant quadratic and cubic components of biomass curves was unsuccessful. An attempt to eliminate the effect of different initial biomass levels on rate of decline was made by comparing the slopes of rate of biomass decline between species, and relative rate (rate per unit biomass) of decline between species, but transformation obscured effects rather than clarifying them.

To resolve this problem and highlight the stages when consumption of aspen changed in relation to the consumption of the other three species, a three-way factorial analysis of variance was conducted on the biomass data, separating the effects of replication, species and days-grazing and using the three-way interaction for error. From this analysis a Student Newman Keuls' range test (Steele and Torrie 1980) was conducted on the differences in biomass between aspen and each of the other species, on each grazing day (Tables V.3 and V.4).

In 1979 (Table V.3), while the difference in biomass between aspen and rose and raspberry remained constant, indicating that they were removed or trampled at the same rate, the biomass difference between aspen and snowberry changed significantly. With early grazing 1979, it became significantly larger on day 7 than it had been from commencement to day 4. From Figure V.3 it is apparent that the curves for aspen and snowberry were parallel up to day 4, when aspen began to diverge so that by day 8 the difference between the curves was significant. The same delay in decline in aspen till day 5 was apparent with early grazing 1980 (Table V.4).

With late grazing 1979 (Table V.3), the difference between aspen and snowberry biomass declined until day 4 (aspen was being consumed faster than snowberry), after which time the difference increased again (aspen removal slowed while snowberry removal increased). By day 8, the difference was significantly greater than it had been at day 4. The accelerated removal of snowberry compared to aspen was evident again with late grazing 1980 (Table V.4). The earlier grazing of aspen was not apparent at this time, perhaps because there was very little aspen present to graze. Hence, in 1980 late, all the comparisons were akin to a comparison of absolute means within a species. The same is true of comparisons with rose and raspberry in 1980 early.

Table V.3 Student Newman Keuls' range test on differences between biomass (kg ha^{-1}) of aspen and other species over the early or late grazing periods in 1979

		Comparisons		
Grazing per.	Day	Asp-Rose	Asp-Raspberry	Asp-Snowberry
1979 Early	1	67.0	26.2	-73.5 a
	3	73.0	44.9	-71.8 a
	4	67.5	46.7	-78.7 a
	5	74.3	49.7	-86.8 ab
	6	64.9	42.6	-102.3 ab
	7	41.4	22.5	-119.5 b
	8	30.4	13.0	-135.6 b
	9	24.8	15.1	-143.6 b
	10	22.7	15.6	-146.1 b
	11	16.6	11.8	-144.1 b
	12	17.1	12.6	-144.1 b
Std. Error		13.7	13.7	13.7
1979 Late	0	285.8	664.7	351.5 abc
	1	318.4	650.8	326.9 abc
	2	286.0	624.6	301.7 ab
	3	274.2	629.7	298.5 ab
	4	243.0	627.0	287.7 a
	5	215.7	623.7	302.2 ab
	6	204.8	618.1	371.0 abc
	7	189.8	604.7	385.1 abc
	8	199.7	613.0	445.6 bcd
	9	199.7	634.5	460.7 cd
	10	190.4	628.1	527.7 d
Std. Error		34.3	34.3	34.3

Means within columns, within grazing periods, without following letters, or followed by the same letter, are not significantly different ($P<0.05$).

Table V.4 Student Newman Keuls' range test on differences between biomass (kg ha^{-1}) of aspen and other species over the early or late grazing periods in 1980

		Comparisons		
Grazing per.	Day	Asp-Rose	Asp-Raspberry	Asp-Snowberry
1980 Early	1	416.6 a	418.2 a	171.9 a
	2	420.6 a	419.3 a	171.6 a
	3	421.0 a	416.4 a	170.0 a
	4	416.8 a	413.0 a	162.6 a
	5	410.7 a	410.5 a	151.6 a
	6	382.5 ab	385.9 ab	125.2 ab
	7	356.2 abc	360.2 abc	94.6 abc
	8	334.0 bcd	336.6 abcd	69.3 bc
	9	314.6 bcd	321.9 bcd	48.3 c
	10	299.1 cd	306.4 cd	33.7 c
	11	301.4 cd	306.4 cd	33.7 c
	12	287.3 cd	291.7 cd	49.6 c
	13	258.4 d	262.9 d	41.1 c
Std. Error		19.0	19.0	19.0
1980 Late	0	-478.8	-248.4	-346.5 a
	1	-475.0	-246.9	-345.9 a
	2	-474.1	-238.5	-344.4 a
	3	-479.4	-239.2	-346.0 a
	4	-480.2	-207.9	-320.7 a
	5	-477.7	-182.7	-279.0 a
	6	-470.4	-174.3	-227.3 b
	7	-487.9	-174.0	-188.0 b
	8	-487.9	-174.0	-188.0 b
Std. Error		19.5	19.5	19.5

Means within columns, within grazing periods, without following letters, or followed by the same letter, are not significantly different ($P<0.05$).

Palatability indices

Palatability indices calculated for each species on each day of each grazing period are shown in Appendix E. These indices attempt to correct for differences in the composition of the plant community, and should be a more stable representation of palatability than slopes describing biomass disappearance.

The slopes of linear regressions of palatability indices on days-grazing were tested by least squares regression. Table V.5 shows the coefficients for that analysis, and least squares means adjusted to the covariate value zero (the regression intercept) and to the covariate mean, this being the best estimate of the palatability index of each species over the whole grazing period at each time of grazing. Coefficients of determination are shown, and indicate the high degree of variability associated with these palatability coefficients.

Palatability of individual species, before browsing (Table V.5 - intercept), was influenced by both season of grazing, and age of stand. Rose was relatively more palatable early in the season than late. Its palatability was lowest late in the second year, by which time it had developed woody stems. Aspen was relatively more palatable late in the season than early, the effect being more marked in the older stand of 1980. Raspberry remained relatively palatable, regardless of season or stand age. This is not surprising, since, in 1980, regrowth consisted of new shoots

Table V.5 Regression coefficients (b_1) and means adjusted to covariate zero (intercept), and to the covariate mean (mean), with standard errors, for linear regressions of palatability index on days grazing.

	Coefficients and Means						
Treatment	b_1		Intercept		Mean		r^2
1979 Early							
Aspen	.0141 a	.03	.63 b	.19	.70 c	.08	.01
Rose	.0666 a	.04	1.22 a	.21	1.57 a	.10	.16
Rasp.	.0154 a	.02	1.09 a	.16	1.17 b	.07	.01
Snowb.	.0167 a	.04	.23 c	.24	.32 d	.11	.00
1979 Late							
Aspen	-.0566 b	.02 *	.79 bc	.12	.50 b	.06	.53
Rose	-.0895 a	.03 *	1.05 b	.14	.59 b	.06	.26
Rasp.	-.0851 ab	.02 *	1.74 a	.12	1.31 a	.06	.24
Snowb.	.0920 c	.02 *	.50 c	.12	.96 a	.06	.51
1980 Early							
Aspen	.0823 a	.03 *	.12 b	.21	.58 c	.09	.18
Rose	-.0353 b	.04	2.07 a	.24	1.88 b	.13	.05
Rasp.	.1333 a	.05	2.44 a	.25	3.18 a	.14	.03
Snowb.	.0955 a	.04	.18 b	.39	.71 c	.22	.17
1980 Late							
Aspen	-.0059 a	.05	2.25 a	.25	2.22 a	.11	.01
Rose	-.0777 a	.04	.67 bc	.19	.36 d	.09	.15
Rasp.	-.0288 a	.04	1.19 b	.18	1.07 b	.08	.03
Snowb.	.1350 a	.05 *	.10 c	.23	.65 c	.09	.47

Coefficients and means within grazing times followed by the same letter are not significantly different ($P<0.05$).

* b_1 coefficient different from zero ($P<0.05$).

r^2 significant if greater than 0.12 ($P<0.05$, 30 df).

from below ground. Ungrazed snowberry always had the lowest relative palatability.

Browsed plants showed much the same relative palatability as did unbrowsed plants (Table V.5 - mean), with the notable exception of snowberry in late 1979.

As plants are progressively defoliated, one would expect a decline in their relative palatability as their more palatable portions are removed. Slopes of regressions (Table V.5 - b_1) illustrate palatability changes during progressive defoliation. Differences between slopes were established in grazing times 1979 late, and 1980 early. In 1979 late, the palatability of rose during the grazing period declined more than aspen. Also, while the relative palatability of aspen, rose and raspberry declined, that of snowberry increased as forages became sparser. In 1980 early, the palatability of rose declined, while the other species increased. The apparent increase in relative palatability of snowberry in 1980 late was not significant by an F test.

To ensure that absence of some species towards the end of a grazing period was not resulting in unduly high mean palatability indices for remaining species, the indices for the first five days of the grazing period were analysed separately. Results did not alter the relative palatability of species, except that the mean index for snowberry in late 1979 became equal to rose and aspen. Clearly, the high mean palatability of snowberry (Table V.5) arose after day 5, when other forages were becoming scarce.

D. Discussion

Aspen was more acceptable to cattle in the older (1980) stand, while rose was less acceptable (Table V.5). Aspen was more acceptable, relative to other species, when grazed late in the growing season than early (Figure V.4 and Table V.5). This increase in acceptability of aspen, both between seasons and between years, is consistent with the findings of Bryant and Kuropat (1980) who showed that young shoots of woody shrubs were avoided by moose. Such shoots had a higher content of resins than older shoots and selection of shrubs by moose was strongly negatively correlated with the concentration of such resins, and hence, age of shoot. Smith *et al.* (1972) also observed that range cattle browsed aspen more readily in the second half of the growing seson.

In early-grazed treatments, very little aspen was consumed or trampled until day 5 whereas in late-grazed treatments browsing commenced on day 1 (Figure V.4 and V.6). This acceptability of aspen late in the growing season, relative to other forest species, makes autumn defoliation of aspen by cattle less difficult to accomplish. Similarly, the apparent readiness of cattle to graze within the forest, as opposed to the adjacent grassland, late in the season, is convenient if one wishes to maximise browsing at the end of the season. Hilton and Bailey (1972) observed that cattle tended to graze within the forest during dry spells, and suggested that animals were selecting the moister forage. More recently, Gesshe and Walton (1981) found a strong positive correlation between moisture content and selection by cattle of mature forages. On this basis, dry fescue grassland in August in this study would be relatively less palatable than the much more lush green grassland early in the season.

Rose and raspberry were highly palatable as young shoots in the first year, and raspberry continued to be favoured in the second year. The difference in palatability between these species in 1980 may arise because rose grew a woody stem from which small new shoots arose after each grazing, while raspberry produced new shoots from underground rhizomes, and these shoots, being current growth, had no woody stem.

Snowberry was unpalatable in all seasons but, after initial avoidance, was grazed much more readily late in the season than early. Again, this may be related to the concentration of resins in young and old foliage.

Some of the conclusions about animal preference can be gleaned directly from the biomass curves without further recourse to the indices. These curves are most useful for observations about the stage at which species become acceptable or unacceptable. However, they do not separate the characteristic of species palatability from relative availability, and hence, their use in extrapolation to a community where the four species are in proportions outside the "within season" range of this study (Table V.1) would be decidedly risky.

The palatability indices are independent of relative availability which makes them much more amenable to extrapolation.

In the development of the index, daily consumption is assumed to be the weight of plant material removed each day. Material removed by trampling is assumed to be proportional to the amount consumed. Gesshe and Walton (1981) also calculated consumption from grazed and ungrazed swards. The error associated with trampling would be more constant between species of forage of similar structure (Gesshe and Walton 1981) than between the components of regenerating aspen forest. In most cases where preference indices have been calculated, diet composition is established by the use of oesophageal fistulae (Van Dyne and Heady 1965, Rosiere *et al.* 1975b); Laycock *et al.* (1972) found it more accurate than comparing grazed and ungrazed plants. They recorded trampling loses by sheep, over six days, to be about 50% of the total plant material removed.

From the point of view of brush control, it is the amount removed that is important, whether it is by grazing or trampling. Perhaps, in this case, the indices might be better termed "cattle removal" indices, or, as in southern U.S. (R.E. Sosebee, personal communication), "forage disappearance" indices.

Table V.6. Preference indices - PI (Van Dyne & Heady 1965), and correspnding palatability indices (PAL) for four species during four grazing seasons, showing ranking.

Treatment	Spp.	P.I.	Rank	S.E.	PAL.	Rank
1979 Early	Aspen	.67	3		.70	3
	Rose	4.46	1	1.3	1.57	1
	Raspberry	1.01	2		1.17	2
	Snowberry	.53	4		.32	4
1979 Late	Aspen	.63	4		.50	4
	Rose	.67	3	1.5	.59	3
	Raspberry	2.09	2		1.30	1
	Snowberry	2.13	1		.96	2
1980 Early	Aspen	4.13	3		.58	4
	Rose	5.44	2	1.6	1.88	2
	Raspberry	9.23	1		3.18	1
	Snowberry	.65	4		.71	3
1980 Late	Aspen	3.61	1		2.22	1
	Rose	.49	4	1.7	.36	4
	Raspberry	1.97	2		1.07	2
	Snowberry	1.56	3		.65	3

It is of interest to compare the indices calculated here with those calculated by the procedure of Van Dyne and Heady (1965)[3]. Table V.6 shows indices calculated by both procedures. Generally, the ranking of species by the two systems was similar. Some notable differences occurred when relative availability of component species was substantially different, with low yields being associated with enlarged "P.I." indices. The procedure of Van Dyne and Heady (1965) would seem to be most suited to cafeteria-type trials in which forages are offered in approximately equal quantities.

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[3] Van Dyne and Heady (1965) used "the ratio of the amount of a plant in the diet to the amount available on the range" as an index of preference. As adapted here for a given plant species it was the ratio % removed : % available.

The slopes of the palatability indices for the various species (Table V.5) tended to converge, with the less palatable species, snowberry, demonstrating increasing palatability through the grazing period, and the more palatable species, especially rose, declining or remaining constant. Palatability is considered to be a characteristic of plants, while preference is an attribute of the animal. However, palatability can only be indexed through the senses of the animal. Ellis *et al.* (1976) have considered that, for foraging animals, as food availability declines in relation to the requirements of the animal, their satiation level declines, and they become less selective. Such a development was apparent here, when the diet expanded to include snowberry, as defoliation altered the character of the more palatable species, precipitating a decline in their palatability.

VI. ASPEN SUCKER GROWTH AND ITS EFFECT ON ROOT CARBOHYDRATE

A. Introduction

In the roots of aspen, after shoot primordia initiation, non-structural carbohydrates (mainly sucrose, raffinose sugars and starch; Nelson and Dickson 1980) provide the energy for primordia and shoot growth (Tew 1970, Schier and Johnston 1971, Schier and Zasada 1973). Since top removal stimulates suckering (Farmer 1962, Schier and Smith 1979), it may result in a lowering of reserve carbohydrates, as Donart and Cook (1970) showed with Rocky Mountain shrubs. Schier and Zasada (1973) considered that the rate of utilization of stored carbohydrates will be affected by photosynthesis after shoots emerge above ground. The feasibility of brush control by repeated top removal depends on when, in the development of the young shoot, depletion of root carbohydrates ceases, and replenishment commences. Over 1000 kg ha^{-1} of aspen sucker growth is produced in the first year following overstory removal (Perala 1974), but the contribution of these suckers to root reserve replenishment is unknown, although it has obvious practical importance for brush control operations.

Many of these suckers subsequently die, being dominated by the relatively few successful suckers. On the subdominant suckers, old leaves generally remain green, but production of new leaves ceases. Evidently these suckers are no longer drawing on carbohydrate reserves, since reserves are not completely depleted by one crop of suckers, but take many repeated crops to become exhausted (Berry and Stiell 1978).

The process by which the exploitation of reserves by subdominant shoots ceases is not established.

Two possible explanations are:

1. Low light intensity reduces the growth of the apical meristem. Farmer (1963) found that growth of aspen shoots was slower under light of 500 foot candles intensity than under light of 1700 foot candles, which is approximately 20% of full summer sunlight. Leaves in both treatments became chlorotic while leaves of maize, tomato and bean remained green, suggesting that aspen was less tolerant of shade. Reduced growth may reduce the importance of the apical meristem as a metabolic sink. This may be brought about by a reduced rate of auxin synthesis in the apex and, since auxin stimulates sucrose transport over large distances (Seth and Wareing 1967), a reduced sucrose transport stimulus.
2. The shaded subdominant suckers are receiving light which, as well as being of lesser irradiance, has been subject to differential absorption in the upper story canopy (Holmes and Smith 1975). The resulting light energy is relatively lower in the 400 to 700 nm range than is normal sunlight, and higher in the far red region (>700 nm). This decrease in the ratio of red to far red light under the canopy would be expected to shift phytochrome in plants under the canopy from the

Pfr to the Pr form (Kendrick and Spruit 1977). A change in the Pr:P(total) ratio may influence the mobilisation and transport of root carbohydrates, perhaps by altering sink demands in the shoot.

An experiment was conducted to investigate the loss of carbohydrate in aspen roots, from production of shoots, and the subsequent partitioning between parent root and new shoot, of carbohydrate from photosynthesis of emerged shoots, both dominant and subdominant (shaded). Specifically, the experiment was structured to determine:

1. the effect of clipping of suckers towards the end of the growing season, on total non-structural root carbohydrates (TNC), and
2. the effect of production of shoots from excised aspen root segments on TNC concentration in the root segments of shoots growing in darkness, in light of equivalent quality to normal sunlight (normal), and light of quality equivalent to that under a forest canopy (far red), and
3. the morphology of shoots grown under those light regimes.

B. Methods

Time of top removal

Aspen forest was burned in 1972, and again in May 1979. In early June, before any visible outgrowth of root primordia, it was divided into 2m x 2m plots marked out by narrow trenches 30 cms deep, so that all surface roots were severed between plots. Suckers emerging on these plots were clipped, to 50% of their height, on one of three occasions (July 17, August 7, August 27) during 1979. Control plots were not clipped. There were three replications of the field plots.

Root sampling and preparation

Surface roots (maximum depth 5 cm) from clipped and unclipped plots for the three clipping dates were dug up after onset of dormancy, on 8th October 1979, taking four roots per plot. A 2-3 cm segment was cut from each end of these roots, and was immediately placed in dry ice, prior to analysis for total non-structural carbohydrates (TNC). The carbohydrate concentration of a sub-sample taken from ground and mixed root tissue from the two extremities of an excised root, should incorporate any gradation in carbohydrate concentration along that root.

After removal of segments from the extremities, each root was wrapped in a moistened towel and returned to the laboratory where it was divided into three segments 8-10 cm long. Each segment was labelled, and soaked for 5 minutes in a fungicide solution (2.2% methyl mercury dicyandiamide), to reduce the incidence of infection by pathogens entering through the cut surface. Its ends were sealed with melted paraffin, and finally, it was planted 1-1.5 cm deep in moistened vermiculite (Schier 1978), in one of three growth cabinets. One third of each root was placed in each cabinet.

Light environment treatments

One cabinet was maintained in total darkness. Light in the remaining two was balanced for PhAR at 195 μE[4] m^{-2} s^{-1}, with quanta in the red and far red regions contrasting (Figure VI.1). The spectra were similar in the 400 to 660 nm range. Quality in the "normal" cabinet approximated the quality of normal sunlight, and was maintained by a series of fluorescent lamps. Light quality in the far red enriched cabinet approximated light quality under an aspen forest canopy as recorded on a Tectrum Instruments Quantaspectrometer (QSM-2500) in east central Alberta in June 1979 (Figure VI.2). The light source was similar to the "normal" cabinet, except that some fluorescent lamps were replaced by a high intensity quartz iodide lamp, covered with a red filter. Photoperiod was 16 hours. Temperature was maintained at 25/15 °C for 16/8 hours (Schier and Zasada 1973), and relative humidity at approximately 70%. Plants were watered daily.

After approximately 8 weeks, plants were harvested and shoot growth characteristics were recorded, i.e., total number, number >1 mm, height, weight of shoots, weight of stems , weight of new roots, leaf area. Stems, leaves and roots were then oven-dried to obtain dry weights. Root segments were placed in a deep freeze (-40 °C) prior to analysis for TNC.

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[4] μE: Micro Einsteins.

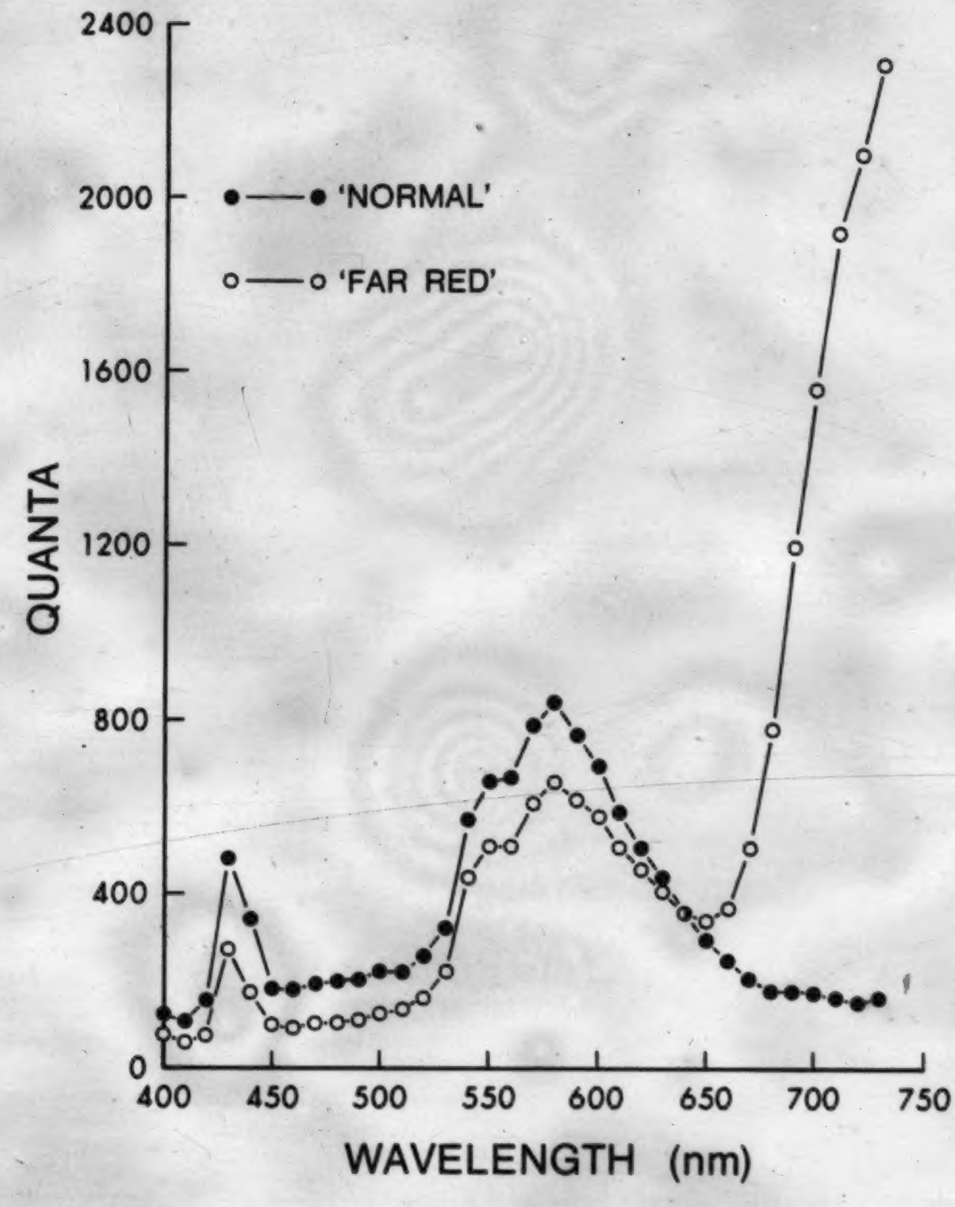

Figure VI.1 Light energy in the 400 to 730 nm range in the normal and far red enriched growth cabinets.

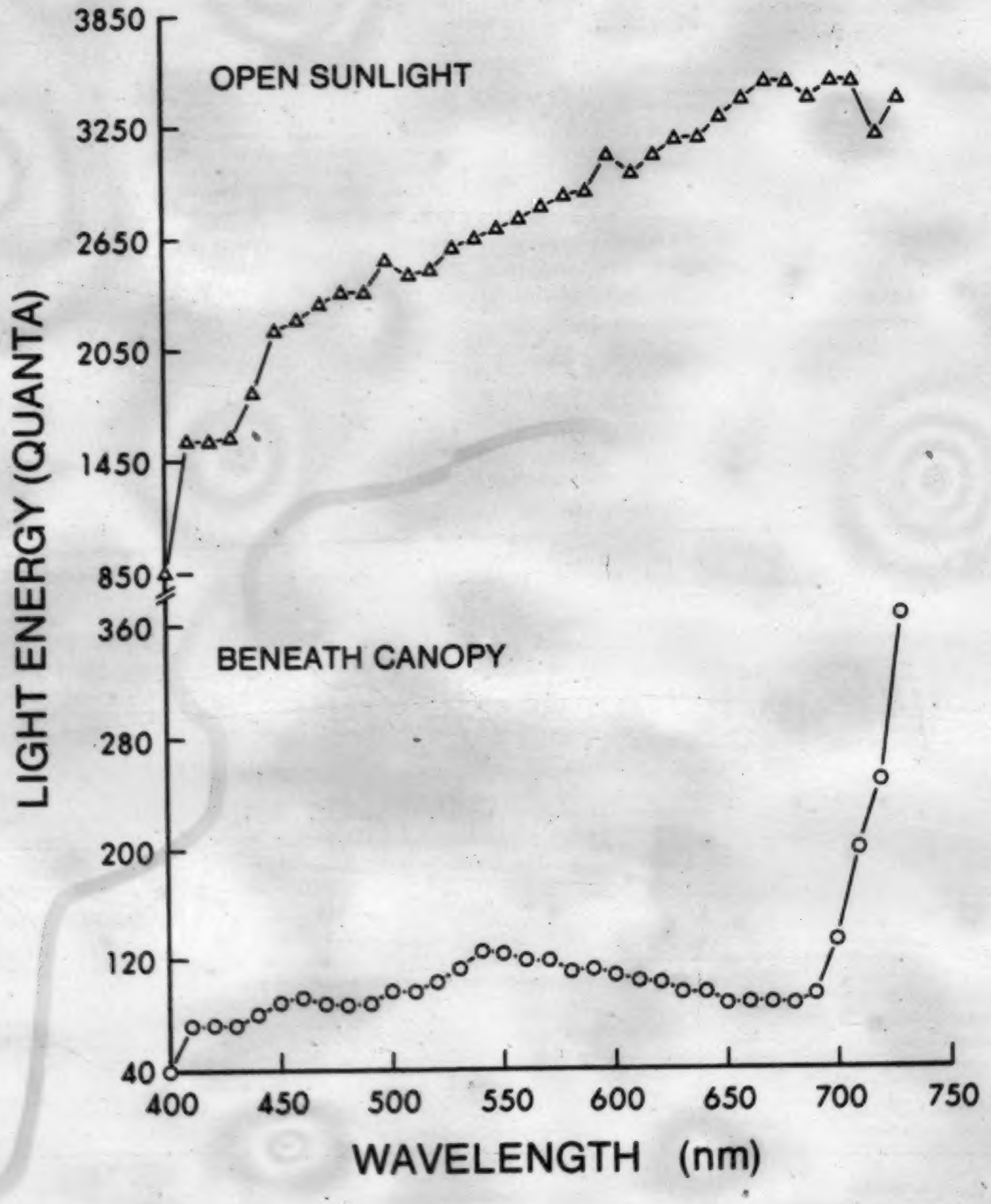

Figure VI.2 Light energy over the 400 to 730 nm range, at Kinsella, Alberta, at 3.30 pm on July 16 1979, in full sunlight, and under an aspen forest canopy.

Anthocyanin detection

Synthesis of the pigment anthocyanin has been shown to be stimulated by red light, the effect being reversed by far red light, and consequently, has been linked to the form of phytochrome (Schneider and Stimson 1971). At equal flux densities, anthocyanin indicates the current form of phytochrome in plants growing under light regimes differing in the 660-730 nm range.

Therefore, following morphological measurements, all stems and leaves from shoots within the light treatments were separated, ground, and a sub-sample of 10 g extracted overnight in an HCl/ methanol solution (1 ml concentrated HCl:100 ml methanol) at 4°C. Absorption of light passing through the extract was read on a spectrophotometer at 525 nm, this being the wave length at which the absorption spectrum peak for anthocyanin occurred.

Carbohydrate analysis

Analysis followed the procedure of Smith (1969). Root tissue was dried in an oven at 100°C for 90 minutes, and then at 70°C for several days. When dry, it was finely ground and a sub-sample digested with α-amylase (Sigma Chemical Co. St. Louis, Mo.) solution for at least 48 hours. To ensure breakdown of fructosans if present, following digestion, solutions were hydrolysed with 0.1N H_2SO_4. Concentration of reducing sugars extracted was determined by spectrophotometry using 3,5-dinitrosalicylate solution as a colouring agent and testing the sample solutions against prepared solutions of known concentrations of glucose/fructose. Concentration of carbohydrates was expressed as % of dry weight of root tissue.

Statistical analysis

The statistical design was a split plot with field treatments split for cabinet treatments as follows:

	D.F.
Rep(R)............	2
Clipping(T).......	3
RT (Error a)......	6
----------------------split	
Cabinets(C).......	2
TC	6
RC	4
RTC...............	11
Total[1]............	34

Due to failure of some roots to produce shoots, there were unequal numbers of roots per treatment, which necessitated the use of a regression approach for analysis of variance. The factor 'T' was tested against 'RT', and 'C' and 'TC' against the sum of 'RC' and 'RTC'.

Where appropriate, the effect of parent root diameter, or new root weight, was included in the model, as a covariate.

Means are least squares means calculated from the coefficients fitted to the regression model.

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[1] One missing cell (RTC) reduced the total D.F. and the 3-way interaction D.F. by 1.

C. Results

Time of top removal

Carbohydrates

Field clipping in July and August, had no significant effect on TNC in roots in October (Table VI.1). Mean TNC at sampling on 8th October was 10.5% by weight. There was a general decline in root TNC associated with shoot growth in growth cabinets (Table VI.1). Time of field clipping did not significantly affect this decline (Table VI.1).

Shoot number

Roots from successively later clipping treatments gave rise to successively fewer suckers (Table VI.2).

A regression of number of shoots (>1 mm) on time of clipping was significant (F=12.7) but with an r^2 of only 0.14. A regression of shoot number including all visible primordia (i.e. everything initiated) on time of clipping explained even less variation (r^2=0.08). Clipping time, then, would appear to be more closely related to shoot outgrowth than to primordia initiation. Schier (1973a) concluded that initiation was controlled by hormones, while outgrowth depended on carbohydrate reserves.

Two interactions (Tables VI.4, and VI.5) indicated that shoots which were totally dependent on stored carbohydrate (grown in darkness), grew more, in number and weight, if they were from roots of unclipped or "early"-clipped

Table VI.1 TNC (% dry weight) and the percent change, for roots of aspen suckers from four clipping treatments, at sampling (pre-treatment) and after growth cabinet treatments.

	Clipping time				
	Nil	July 17	Aug 7	Aug 27	S.E.
Pre-treatment	10.1	10.4	10.0	11.6	5.2
Post-treatment	3.3	4.7	2.7	2.9	1.1
% change	65.5	50.1	69.1	70.5	14.3

Table VI.2 Mean number of shoots per root, growing from excised roots of suckers from four field clipping treatments.

	Clipping time				
	Nil	July 17	Aug 7	Aug 27	S.E.
Number†	7.0 a	7.7 a	5.8 ab	3.9 b	1.1

† Shoots > 1 mm.

Table VI.3 TNC (% dry weight) and the percent change for excised roots before and after growth of shoots under three growth cabinet treatments.

	Light treatments			
	Normal	Far red	Dark	S.E.
Before	10.8	9.8	11.0	1.5
After	3.8	3.5	2.9	1.3
% change	60.6	61.9	68.9	3.0

Table VI.4 Total length of shoots per root (mm) from four field clipping treatments, under three light environments.

Clip treatment	Light treatments†			S.E.
	Normal	Far red	Dark	
Nil	185 a	236 a	971 a	47
July 17	199 a	240 a	760 a	52
Aug. 7	108 a	281 a	236 b	43
Aug. 27	105 a	135 a	404 b	25

†Means within columns followed by the same letter are not significantly different (P<0.05).

Table VI.5 Total weight of stems (mg) of shoots from roots from four field clipping treatments, under three light environments.

Clip treatment	Light treatments†			S.E.
	Normal	Far red	Dark	
Nil	100 a^{1}	81 a^{1}	189 a^{2}	24
July 17	106 a^{1}	106 a^{1}	176 a^{1}	26
Aug. 7	104 a^{1}	74 a^{12}	32 b^{2}	21
Aug. 27	56 a^{1}	88 a^{1}	80 b^{1}	12

†Means within columns followed by the same letter are not significantly different (P<0.05).
†Means across rows with similar superscripts are not significantly different (P<0.05).

suckers, than from later-clipped suckers. Shoots with access to both stored carbohydrates and new photosynthates showed no such effects. Note that weights shown in Table VI.5 do not include leaves.

Clipping time had no effect on any other parameters of shoots produced under the three light environments (Appendix F).

Light environment effects

Phenological development

In both light cabinets plant growth was slow (about 30 g in 2 months). During that time the development of the plants under the two light treatments was not markedly different, no terminal buds having formed in either cabinet.

Carbohydrates

TNC levels declined as shoots were produced in growth cabinets, but neither the final TNC level nor the amount of change were different between cabinet light treatments (Table VI.3).

Shoot morphology

Morphological effects of cabinet treatments are shown in Table VI.6. There were no differences in numbers of shoots (>1 mm) produced per root in each growth cabinet, but when all visible primordia were counted, it became evident that, assuming primordia were equally distributed between treatments at commencement, more primordia were initiated in the dark than in the

Table VI.6 Morphological effects of three light environments on aspen shoots at harvest.

	Light treatments			
	Normal	Far red	Dark	S.E.
Shoot number (>1 mm) (root^{-1})	5.4	6.2	6.8	0.5
Shoot number (all) (root^{-1})	7.0 a	6.8 a	10.5 b	0.7
Av. shoot length (mm)	31 a	40 a	84 b	4.9
Stem wt. (mg DM root^{-1})	91	87	119	8.5
Stem wt. (mg DM mm^{-1})	0.52 a	0.49 a	0.17 b	0.02
Leaf area (cm^2 shoot^{-1})	7.9	6.8		1.3
Leaf wt. (mg DM root^{-1})	199 a	134 b		14.6
Leaf wt. (mg DM cm^{-2})	7.7	7.9		1.2
Leaf:stem	2.19 a	1.58 b		0.1
Total shoot wt. (mg DM root^{-1})	294 a	222 b	119 c	22
New root wt. (mg DM root^{-1})	43.7 a	19.0 ab	0.3 b	6.8
Shoot:root†	6.7 a	11.7 a	396.7 b	79

† arithmetic means.

light treatments.

Dark-grown shoots were taller but lighter (thinner) than were light grown shoots. While stem weights were not significantly different among the three light treatments, a greater weight of leaves was produced per root in normal light than far red light, which meant that total shoot weight per root was heaviest in normal light, lightest in the dark, and intermediate in far red light. The leaf:stem ratio reflected the greater weight of leaves under "normal" light.

New roots were heaviest in normal light, lightest in darkness, and intermediate in far red light. Resultant shoot:root ratios indicate the partitioning of carbohydrates in dark-grown plants, towards top growth.

In an attempt to explain some of the variation in TNC, the diameter of each excised root was used as a covariate with TNC change. The 6% of variation removed by the covariate was significant but ranking and significance of means was unaltered. Regression of root diameter with TNC at commencement was significant, but only explained 8% of TNC variation ($r^2=0.08$).

When effects of root growth were removed by using dry weight of roots as a covariate with morphological parameters, generally, there was no change in ranking or significance of treatments. The exception was dry weight of shoot, where differences were eliminated, though ranking remained the same. The covariate 'root weight' accounted for 26.6% of variation in dry weight of shoot.

Anthocyanin

Anthocyanin content, assessed as percentage transmission at 530 nm of tissue extracts, was greater in leaves than stems for both normal (58 vs. 18%), and far red (36 vs. 16%) treated shoots. There appears to be a greater concentration of anthocyanin in leaves in normal light than in far red light, which supports the expectation that phytochrome existed in different forms in the two light cabinets, and therefore, can be considered as having a possible influence in the morphological effects observed.

D. Discussion

Time of top removal

Aspen plants, in the plots subjected to field clipping, had been burned in the spring, after which, their roots were disturbed by deep ripping. They produced suckers in the latter half of the season. Carbohydrate concentration in the roots of these plants was generally (and not surprisingly) low. The somewhat higher TNC levels (15-20%) recorded by Schier and Zasada (1973) were in undisturbed forests.

Roots from unclipped field plots and from the July-clipped plots that were kept in darkness, produced longer and heavier stem material per root (Tables VI.4 and VI.5) than roots from later-clipped plots. Shoots growing in darkness are dependent on stored carbohydrates. The result suggests that unclipped and early-clipped plants had more carbohydrates available for growth than later-clipped plants. Early-clipped plants may have had sufficient growing season left for some carbohydrate replenishment to take place.

The absence of any such trend in TNC from the laboratory analyses of root TNC casts some doubt on the sensitivity of those analyses. Inaccuracy may have been associated with initial drying of the root tissue.

The process of drying of root material prior to analysis is critical. Raguse and Smith (1965) tested techniques in TNC analysis using enzyme digestion, and reported significant differences in the yield of TNC from drying alfalfa at various temperatures, or freeze-drying, the latter giving the highest, and presumably, the most accurate yield. Smith (1969) reported that, at 100°C, carbohydrate losses will occur once the tissue has reached dryness. At lower temperatures (70°C), the tissue suffers respiratory losses until completely dry.

Where tissue varies in bulk, the time taken to reach dryness will vary. In this experiment, variation in root diameter may have resulted in a variation in the loss of carbohydrates due to respiration or heat breakdown for large and small roots respectively. Freeze-drying would eliminate this problem.

Light environment effects

While small differences in TNC levels between clipping treatments may not have been discernible under the drying procedure which was followed, light treatments each encompassed the full range of variation in root diameter, and consequently, may have a constant level of error across treatments, making comparisons possible.

Carbohydrates

The production of shoots was associated with a lowering of root TNC levels in all three growth cabinets to approximately the same extent (Table VI.3). The final levels were quite low. There is nothing to suggest any contribution from photosynthesis to TNC in parent roots at this stage of development.

It seems that instead of using photosynthates to restore TNC levels, light-grown shoots remained as "sinks" and used their photosynthates for top growth. The excess weight of shoots grown in light over those grown in darkness (Table VI.7) must be attributable to photosynthesis. Shoot weights in far red light were doubled and in normal light almost trebled. The utilisation of photosynthates in the actively growing shoot corresponds with the findings of Larson and Dickson (1973) for *P. deltoides* seedlings up to LPI 9. In the study reported here, leaves were not counted, but they would have been less than 9 in almost all cases. Donnelly (1974) reported similar acropetal transport for

Table VII.7. Comparison of TNC change and shoot growth under growth cabinet light treatments.

	Light treatments		
	Normal	Far red	Dark
TNC loss (%)	60.6	61.9	68.9
Shoot wt. per root (mg)	294	222	119
Av. shoot wt. (mg)	54.4	35.8	17.5
Wt. gain due to photosynthesis (mg)	36.9	18.3	

actively extending branches of mature trees of *P. grandidentata*, with net basipetal transport only commencing in the latter half of the season.

Larson and Gordon (1969) reported that the root system of *Populus deltoides* seedlings absorbed up to 60% of photosynthates exported from mature leaves, and that basipetal transport only became significant after the 6-7 leaf stage. However, the roots of their seedling plants were growing actively. Hence, they were an active metabolic sink, unlike the old excised roots in this experiment.

As Schier and Zasada (1973) found, shoots apparently competed for available substrate. Regressions of shoot weight and shoot number within cabinet treatments revealed a significant negative relationship in the dark cabinet (F=18.9, r^2=0.3) but not in the light treatments. It would appear that photosynthesis was compensating, to a small extent, for competition for carbohydrates among light-grown shoots.

There is no suggestion that phytochrome influenced the mobilisation of root carbohydrates for shoot growth, since there were no differences in root TNC between light environment treatments. Phytochrome may have influenced the efficiency of photosynthesis, perhaps by controlling the rate of transport of assimilates from source to apex, since shoot weights differed between light quality treatments. The promotion of photosynthesis by increasing sink demands, associated with accelerated transport of assimilates, was demonstrated by Peet and Kramer (1980) in soybeans.

Partitioning

Some differences in partitioning were evident. Shoots grown in normal light directed less photosynthate towards producing stem tissue than did shoots in far red enriched light. Instead, they allocated it to the growth of leaves. This was significant when expressed as a leaf:stem ratio, and suggests that phytochrome was controlling stem elongation and leaf growth as an adaptation to shade. Such effects have been reported for other plants (e.g., Mohr 1974 on *Sinapis alba*).

Shoots were heavier in normal than in far red light, even though the two cabinets were subject to equal PhAR. Greater leaf weight in normal light may have been associated with greater total photosynthesis, and a correspondingly greater dry matter accumulation.

Hoddinott and Hall (Can. J. Bot., In press) have found that far red enriched light encourages the growth of tops in bean plants, or conversely, that red light ("normal") stimulates transport of assimilates away from tops.

Since PhAR was balanced in their experiment, one would expect, as was found here with aspen, that there would be relatively less root development under far red light. However, their plants had active root systems, so that water uptake would not be a limiting factor, whereas, in this experiment, it may have limited growth in the far red cabinet. Symptoms of wilting were not obvious. Furthermore, in bean plants, a root system limited by pot size restricts growth through the hormone system, involving GA and cytokinins, and not through water or mineral uptake (Carmi and Hever 1981).

In this experiment, as in that of Hoddinott and Hall, translocation to roots may have been stimulated more under normal than far red light, through light quality effects. The resultant greater root development would have permitted greater top growth through greater hormone synthesis (Carmi and Hever 1981), masking the effect of partitioning towards top growth in far red light, noted by Hoddinott and Hall. Even so, the shoot:root ratio tended to be higher under far red light, which is consistent with the observations of Hoddinott and Hall.

The lack of difference in TNC loss between light treatments could also be associated with the differences in root development. Richardson (1956) showed a positive relationship between available root reserves and subsequent root growth of *Acer saccharinum*. The root development in the lighted growth cabinets may have drawn on TNC reserves which had not been lowered in those treatments as much as in the dark cabinet. In this way light-grown shoots, having stimulated root development, ensured their survival at the expense of TNC reserves. Differential root development, if it occurs in the field, might explain much of the growth rate differences in shaded and unshaded sites.

Only 22% of viable excised roots developed adventitious roots. Undisturbed suckers normally produce very few new adventitious roots at their bases in the initial 2 or 3 years. Zahner and Debyle (1965) found that the suckers remain at least partially dependent on the parent root for up to 5 years, and suggested that the plants were unable to supply water and nutrient needs from the small number of adventitous roots which had developed at their bases.

Limitations of excised roots

The shoots here were grown on excised roots. Schier (1973a) suggested that GA which, in roots, is synthesised in the root tips (Moore 1979), may be low in excised roots. He applied GA to excised aspen roots and found that it inhibited shoot initiation but once outgrowth had commenced it was stimulated by GA. This was reversed by the application of pyrimidine (a GA inhibitor). In this experiment, abundant shoots commenced outgrowth as would be permitted by an absence of GA. Then, where root growth occurred (and GA was synthesised), shoot growth was stimulated. Where there was little root development, shoot growth was slower than one would expect in the field, suggesting an absence of GA, although the rate of water uptake might also be limiting.

The role of cytokinins in the stimulation of localised transport was established by Mothes and Englebrecht (1961), and later, over longer distances in association with GA, by Thorpe and Murashige (1970), and Sharif and Dale (1980a,b). The low concentration of these hormones in excised roots (Schier 1973a) seems likely to result in reduced shoot growth (Carmi and Hever 1981), and reduced translocation of metabolites to roots. Hence the question of the difference in behaviour of excised roots and entire roots in sucker growth makes extrapolation to the field situation in regard to the restoration of root TNC somewhat hazardous, and points to the need for investigation into the movement of metabolites in suckers actually growing in the field.

E. Conclusion

In the initial stages after emergence, while leaves are expanding, aspen suckers are unlikely to begin to restore carbohydrate which has been mobilised to produce those suckers. In this study, net basipetal transfer had not occurred in the two month period, but these suckers were grown at about 20% normal light intensity, and from excised roots. Root systems in suckering aspen might not be active sinks in the first year, since Zahner and Debyle (1965) found little root development in the first few years of a sucker's development. Mature trees only commence basipetal translocation of assimilates after midsummer, when active extension has ceased (Donnelly 1974). It seems likely that young suckers, whose active extension phase lasts longer than in mature trees, will retain their photosynthate for top growth, and be correspondingly later in commencing basipetal translocation.

Evidence to elucidate the process of growth inhibition, and root carbohydrate restoration in shaded plants, is inconclusive. Light quality had no effect on final TNC levels, but it did appear to be controlling some aspects of adaptation to shade. Greater leaf development in plants in normal light enabled those plants to fix more carbon, and consequently grow faster. They also produced more adventitious roots, for which the supply of assimilates may have been light-mediated. Whether root development came first as a response to red light, or after leaf development as a response to increased photosynthate supply, is not known, though the evidence of Carmi and Hever (1981), discussed above, suggests the former.

While there was some evidence that light quality influenced the partitioning of assimilates, with plants grown in "shade" having lower leaf:stem and higher shoot:root ratios, plants under the two light quality treatments were not phenologically different. This suggests that the differences in performance of suckers in the field may be a response to light intensity as well as light quality.

VII. CONCLUSIONS

Range management, as an academic discipline, is essentially the study of the manipulation of plant communities by man to serve a particular set of objectives ranging from the production of domestic animals in the most efficient way possible, to the maintenance of a range of native species for use by wildlife, or even for purely aesthetic purposes. These diverse objectives, and the desired degree of control over the whole ecosystem, must dictate the strategies employed. The complexity of the environment involved may range from one involving many species growing in many strata, to a relatively simple one such as a monospecific grass sward.

In the field study reported here, the plant community and its environment were highly complex with many species competing for the available resources. The study was an attempt to unravel some of this complexity, the objective being to replace trees and woody shrubs with vigorous pasture species in circumstances which did not permit the use of mechanical operations. Such an objective fell well within the scope of the above definition of range management, particularly if the unravelling revealed possible techniques for predictable plant community manipulation, as indeed it did.

The predictable modification of a natural ecosystem requires an understanding of the factors operating in, and controlling that system. In this study, some of the factors controlling the interaction between grazing animals and aspen forest were elucidated; specifically, those relating to selection by the animal, and to regrowth of some of the original and introduced plant components, following heavy grazing. In addition, some of the physiology of regrowth of the dominant plant species was examined.

The dominant species in the plant community studied was aspen. In its native state, aspen is an important forage resource for many species of wildlife from large ungulates to many birds and insects. Elimination of aspen from a wild range would pose a serious threat to many of these life forms. Cattle are not native to North America and do not use all the available species. Consequently, the efficient raising of cattle in large numbers must involve the replacement of the native communities with vegetation suitable for cattle, or at least the modification of those communities.

Mature aspen forest has little accessible forage for cattle, but the same is not true of aspen suckers. Although little use was made of the foliage of suckers in the first few days of the grazing early in the growing season, the cattle made considerable use of them in late August, and had consumed over 40% of available aspen browse after only four days. The grazing pressure in those late-grazed paddocks at four days was the equivalent of between 0.5 and 0.6 animal units ha^{-1} over the whole grazing season which is not unrealistic. The grazing pressure was, of course, very concentrated which allowed little selection later in the grazing period. Selection opportunities in the early stages would be greater than in a paddock where selection of the most palatable species was taking place over the whole season.

It is only possible to speculate on the reason for the seasonal difference in acceptability of aspen foliage early and late in the season. The changing acceptability of alternative forages, particularly the fescue grassland, seems very likely to be a major cause (Gesshe and Walton 1981). The reason for its avoidance early in the season may be associated with its resin content at that stage (Bryant and Kuropat 1980).

The nutritional value of this foliage is uncertain, since no animal liveweight data were taken. Indications from previous unpublished research (Trabysh and Bailey, personal communication) are that it may be fairly nutritious, having 13% crude protein and 34% crude fibre (acid detergent) in August. The only work which has emerged on digestibility of aspen was at the University of Minnesota on aspen bark which was only 37% digestible (Fullinwider 1976). The foliage would be somewhat more digestible than this. At any rate, as a forage resource for beef production, aspen is likely to be short term, and is unlikely to be as satisfactory for cattle forage as grass species which replace it .

From the aspect of beef production, the interesting point is, not whether aspen foliage is nutritious, but rather, the fact that its acceptability is greater at the end of the season than earlier. Such a change in acceptability is extremely fortuitous in the light of the contrasting effects which emerged from different seasons of grazing.

A substantial degree of control over plant succession in a regenerating aspen forest emerged from grazing season treatments. It was possible, by changing the season of defoliation, to radically and consistently alter the type of plant community which developed, especially the population of aspen suckers, which was the major objective. It now seems theoretically possible, given a particular set of objectives, to dictate the type of plant community which regenerates after a fire in an aspen forest by strategic timing of heavy grazing.

With the present state of knowledge of the effect of season of defoliation on the various individual species, the prediction would be crude. Much more information is needed, not only about the effects of defoliation on those species *per se*, but, just as importantly, about the resultant reactions in the competitive environment of the whole plant community. This study merely laid some foundations for this type of research.

The herbage yield in the plant community emerging after the elimination of aspen probably was well below the maximum potential yield for an improved pasture in that area. It had a large proportion of other woody shrubs with varying degrees of acceptability to cattle. Consequently, a single heavy grazing should not be construed as a total management strategy. Additional grazing during the growing season could be timed to precipitate a decline in certain other shrubs, finally leaving only the introduced grasses. Alternatively, other forms of shrub control (mechanical, herbicides, fire) may be useful as an adjunct to grazing operations, in order to arrive at a productive forage sward.

Probably the major obstacle in this regard is the persistence of western snowberry. There was no evidence of a decline under the treatments imposed in this study. In fact, it may have expanded as grazing removed its competitors, as suggested by plant density data (Table III.7). Overall manipulative control has not been achieved until the problem of western snowberry has been overcome.

Cattle were used in this study, because they are the most abundant domestic animal species in the aspen parkland of western Canada. Other species of animal may be more effective for aspen defoliation. Sheep graze aspen more readily than cattle (Sampson 1919, Smith *et al*. 1972). Elk are known to decimate aspen stands in areas where they are concentrated (Gruell and Loope 1974). Goats are very heavy browsers, but may eliminate desirable herbage as well (Sheldon 1980). A strategy which was found satisfactory using cattle, may be even more effective with one or more of these alternative animal species.

The establishment of introduced grasses was enhanced by removal of shrub competition early in the growing season as opposed to allowing newly established seedlings to try to compete with vigorously regenerating shrubs until the end of the season. However, while early grazing aided grass establishment, and indeed a respectable sward established, making up 28% of total biomass in the second year, there was no noticeable depression of aspen suckers as a result of the presence of this vigorous sward. Failure to suppress aspen suckers under early grazing prevented further expansion of grasses in the third season. Where aspen had been eliminated (under late grazing), although initial establishment of grasses was poorer, they gradually expanded. By the third season the grasses were contributing as much under late grazing as in the better established early-grazed swards. If aspen was preventing the expansion of grasses, rather than the reverse, attempts to control aspen regrowth following overstory removal, simply by introducing competing grasses, seem unlikely to be very fruitful.

The picture emerging is one of two conflicting needs. The control of aspen suckers requires late season grazing, but the establishment of grasses, so essential for long term range development, requires an early grazing. Some combination of the two may be effective in achieving both objectives. However, the result is by no means a foregone conclusion. The early grazing of aspen may cause it to branch in such a way that complete defoliation in August is difficult. Again, the late grazing of forage seedlings, in addition to their early grazing, may have a detrimental effect on their vigour and perhaps their ability to survive the winter. Further investigation is necessary.

In Chapter III, the possible reasons for the dramatic effect of late defoliation on aspen suckers was discussed at length. In relation to the need for complete defoliation, it should be emphasised that practically complete defoliation was achieved by that treatment, and if the dormancy inhibition theory proposed in Chapter III is correct, the presence of some leaves may allow the establishment of dormancy in enough of the plant to permit its survival. Again, total defoliation does not necessarily have to be achieved by cattle. Mechanical defoliation, or a chemical defoliant, might achieve the same result, or supplement the grazing technique.

The movement of carbohydrate in the roots of aspen, as suckers are produced, emerge, and grow, was found to be consistent with published evidence about source/sink relationships in actively growing plants. It was not consistent with the frequently stated view that restoration of carbohydrate reserves commences once suckers emerge. Considerable time may elapse before any such restoration occurs since actively growing shoots are likely to retain most of their photosynthate for shoot growth. If stems continue to elongate until just before leaf fall, as *Populus* sucker stems frequently do (Kozlowski and Keller 1966), little or no replenishment of carbohydrate can be expected in that growing season. Consequently, annual top removal carried out in June with the objective of depleting carbohydrate reserves, may be sufficiently frequent to prevent any carbohydrate replenishment. With more frequent top removal, carbohydrate depletion associated with submerged sucker initiation and growth, would be more frequent, but little or no carbohydrate replenishment may be expected in either case.

As previous published work showed, annual top removal operations are slow to reduce suckering, and laborious to carry out. There was no evidence of a decline in suckering vigour after two heavy early grazings, and none could be expected for at least 4 or 5 years (Berry and Stiell 1978, Perala 1979).

Carbohydrate reserves in roots of established aspen clones seem to be adequate to supply a number of crops of suckers. Attempts to control aspen by exhausting these reserves has not been successful in the short term. Investigations into the causes of control by August defoliation are likely to be more rewarding.

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IX. APPENDICES

A. The influence of aspect and slope

Aspect and slope play an important part in plant community succession in the aspen parkland (Moss 1932, Bird 1961, Scheffler 1976). Therefore, a description of the slope and aspects of the individual experimental paddocks is necessary to fully explain all botanical changes.

Replication 1 "early" was a steep (45°) north-facing slope and extended almost to the top of the slough.

Replication 1 "late" had a northerly aspect but a much less marked slope, the lower portion of which was practically level, with a portion sloping gently eastward.

Replications 2 and 3 almost encircled a slough which was elongated in a NNE/SSW direction.

Replication 2 "early" was on the south-west edge, and faced north-east but had only a very gentle slope. Part of the paddock actually sloped gently towards the south-east.

Replication 2 "late" was on the north-western side of the slope and had only a very gentle south-easterly slope.

Replication 3 "early", on the north-eastern side of the slough, sloped fairly steeply towards the west.

Replication 3 "late" on the south-eastern side of the slough, also sloped a little less steeply to the west.

Analysis of overall yield data revealed some differences between experimental paddocks (Table 1). In 1979, replication 2, which had the most southerly aspect,

Table 1. Total aerial biomass of regenerating forest, for 3 replications of early- and late-grazed treatments on 5 sampling dates.

Grazing season	Rep.	July 1979	August 1979	May 1980	August 1980	July 1981
EARLY	1	1447 b		1685 a	2978 a	4422 ab
	2	2101 a		2075 a	3148 a	4525 ab
	3	1511 b		2206 a	3534 a	5378 a
LATE	1		4093 a	1985 a	3755 a	3942 b
	2		4370 a	1967 a	4099 a	4719 ab
	3		3470 b	1158 b	3620 a	3714 b
Mean		1686	3978	1846	3522	4450
Std. Error		205		214	362	297

Means within columns followed by the same letter are not significantly different (P<0.05).

Table 2. Botanical composition (% by weight) of regenerating forest, for three replications of early- and late-grazed treatments determined from May and August samplings in 1980.

Species	Grazing season	Replication 1	Replication 2	Replication 3	S.E.
Aspen	Early	32.6	23.5	30.1	4.0
	Late	3.5	1.4	2.4	
Rose	Early	6.8	9.2	12.0	4.4
	Late	21.4	21.1	13.3	
Snowberry	Early	6.2	30.5	14.3	4.9 **
	Late	42.4	39.7	20.1	
Grass†	Early	29.1	25.5	28.1	3.7
	Late	17.4	14.3	23.0	
Other spp.	Early	25.3	11.3	15.5	3.9 **
	Late	15.2	23.4	41.1	

** Rep.x Grazing season interaction significant (P<0.01).
† Includes alfalfa.

yielded significantly more dry matter than the other replications. The west-facing slope (replication 3) yielded less than the other replications.

In May 1980 and July 1981, the highest dry matter yield was in replication 3 early and the lowest in replication 3 late. Since these paddocks had similar aspects with only small differences in slope it is difficult to explain the variation without micro-climate data, especially soil moisture.

Analysis of botanical composition data within species, collected during 1980 (Table 2) and in July 1981 (Table 3), revealed some replication X grazing treatment effects which highlight some of the effects of topography on plant community development.

In 1980, the effect of topography had not developed to the extent later revealed in 1981. The only significant replication X treatment interaction was with snowberry and with "other species", i.e., mainly willow, raspberry, and forbs. The snowberry interaction revealed a significantly lower yield on the north-facing slope of replication 1 early than in other paddocks. The "other species" interaction was a combination of a higher yield of willow on that same north-facing slope than elsewhere, and a higher contribution of raspberry on the west-facing slope of replication 3 late.

These effects on willow (other woody) and raspberry were identified separately in the 1981 data (Table 3).

Table 3. Botanical composition (% by weight) of three replications (rep) of early and late grazing treatments in July 1981, for species with significant rep or rep X treatment effects.

Species	Rep.(R)	Grazing season Early	 Late	Std. Error	R
Aspen	1	42.6 a	0.6 c		
	2	19.9 b	4.2 c	3.3	*
	3	36.7 b	3.0 c		
Rose	1	4.0 b	20.6 cd		
	2	12.6 a	30.3 c	4.1	*
	3	11.3 ab	9.5 bd		
Raspberry	1	0.5 b	3.1 ab		
	2	4.2 ab	2.7 a	1.6	*
	3	4.8 a	8.0 a		
Snowberry	1	5.9 c	43.1 a		
	2	25.8 a	29.4 a	5.2	
	3	15.5 ab	24.8 b		
Other woody	1	13.8 a	0.5 b		
	2	0.0 c	0.0 c	1.1	**
	3	1.8 b	0.7 b		
Brome g.	1	7.2 b	6.3 bc		
	2	10.9 b	4.1 c	1.8	**
	3	6.5 b	17.9 a		
Vetches	1	4.8 bc	2.4 b		
	2	1.6 cd	6.1 ab	1.3	
	3	1.1 d	6.8 a		
All herbaceous	1	33.1 a	32.0 a		
	2	37.5 a	33.3 a	4.7	
	3	29.7 a	53.9 b		

Means of species within columns or rows followed by the same letter are not significantly different ($P<0.05$).

** Rep. difference significant ($P<0.01$).

* Rep. difference significant ($P<0.05$).

In 1981, the north-facing slope of replication 1 early grew a relatively lower proportion of rose, raspberry and snowberry, and relatively more aspen and willow. The warmer south-facing slope (replication 2) grew a higher proportion of rose than the other paddocks. The west-facing slope of replication 3 grew the highest proportion of raspberry.

The relatively high proportion of brome grass in replication 3 late was associated with reduced shrub competition (low proportions of aspen and rose), which allowed room for expansion of grasses.

Vetch was of minor importance overall, but the environment in which it occurred is interesting. While generally it was maintained under late grazing, the yield on the relatively level paddock in replication 1 late was low. Early grazing practically eliminated vetch in paddocks with southerly aspects, but it survived much better on the cooler north-facing slope of replication 1 early.

Finally, it is of interest to note, that the contribution of herbaceous species was greatest on the paddock with the lowest overall yield (replication 3 late).

B. *APL* programme for height to weight calculation

The following *APL* programme converts a matrix of <u>height</u> measurements to estimates of dry weight per plant (g). Appropriate intercepts, b_1, b_2, and b_3 coefficients were taken from Tables II.5 and II.6, and manually inserted into *MAT*.

```
       ∇SELP[⎕]∇
      ∇ SELP MAT;M1;M2;M3;MAT0;PH;PHSQ;PHCU;B1A;B1B
[1]    M1←(⍴MAT[1;;])⍴MAT[1;1;]
[2]    M2←(⍴MAT[1;;])⍴MAT[2;1;]
[3]    M3←(⍴MAT[1;;])⍴MAT[3;1;]
[4]    M1←,M1
[5]    M2←,M2
[6]    M3←,M3
[7]    MAT0←(⍴MAT[1,2,3;;])⍴M1,M2,M3
[8]    PH←(⍴MAT0)⍴(MAT[1,2,3;;]÷MAT0)
[9]    PHSQ←PH*2
[10]   PHCU←PH*3
[11]   B1A←⎕←MAT[4;1;]
[12]   B1B←⎕←MAT[4;2;]
[13]   B1C←⎕←MAT[4;3;]
[14]   B1D←⎕←MAT[4;4;]
[15]   B2A←⎕←MAT[4;5;]
[16]   B2B←⎕←MAT[4;6;]
[17]   B2C←⎕←MAT[4;7;]
[18]   B2D←⎕←MAT[4;8;]
[19]   '+++++++++++++++++++++++++++++++++++++++++++++'
[20]   B1←(⍴PH)⍴(B1A+(B1B×PH)+(B1C×PHSQ)+(B1D×PHCU))
[21]   B2←(⍴PH)⍴(B2A+(B2B×PH)+(B2C×PHSQ)+(B2D×PHCU))
[22]   'WEIGHT (GRAMS PER PLANT)'
[23]   W←⎕←(⍴PH)⍴((B1×MAT0)+(B2×(MAT0*2)))
      ∇
```

C. *BASIC* programme for palatability indices

The following *BASIC* programme calculates palatability indices from daily biomass and availability data.

```
: %GET FORAGE
? L
 10 PRINT "FORAGE SELECTION"
 20 PRINT "PALATABILITY COEFFICIENTS"
 30 PRINT "+++++++++++++++++++++++++"
 40 PRINT
 50 PRINT "NUMBER OF FORAGES IS 4"
 60 N=4
 70 *INPUT N
 80 DIM P(9).Q(9),C(9).P1(9)
 90 P9=0
 100 B9=0
 110 Q9=0
 120 C9=0
 130 PRINT "INPUT BIOMASS. UTILIZATION"
 140 PRINT
 150 PRINT "BIOMASS"
 160 FOR I=1 TO N
 170 INPUT B(I)
 180 NEXT I
 190 PRINT "UTILIZATION"
 200 FOR I=1 TO N
 210 INPUT C(I)
 220 B9=B9+B(I) /* TOTAL BIOMASS
 230 C9=C9+C(I) /* TOTAL CONSUMPTION
 240 E9=E9+B(I)
 250 NEXT I
 260 REM PROPORTIONS
 270 FOR I=1 TO N
 280 C(I)=C(I)/C9 /* RELATIVE CONSUMPTION
 290 B(I)=B(I)/B9 /* RELATIVE BIOMASS
 300 NEXT I
 310 REM ITERATIONS TO FIND STABLE PALATABILITY COEFFICIENT
 320 FOR T=1 TO 200
 330 FOR I=1 TO N
 340 IF E(I)=0 THEN: E(I)=1
 350 P1(I)=C(I)*E9/E(I)
 360 P(I)=(P(I)+P1(I))/2
 370 E(I)=P(I)*B(I)
 380 NEXT I
 390 E9=0
 400 FOR X=1 TO N
 410 E9=E9+P(X)*B(X)
 420 NEXT X
 430 NEXT T
 440 PRINT
 450 PRINT "RESULTS"
 460 PRINT "========================"
 470 PRINT "FORAGE"."PALATABILITY"
 480 FOR I=1 TO N
 490 PRINT
 500 PRINT I.P(I)
 510 NEXT I
 520 END
& End-Of-File
: %0
```

University of Alberta

D. Analysis of species biomass during the grazing periods

These analyses of variance are for 4 species and 3 replications, using the covariate "Days-grazing" and testing covariate/species interactions.

```
                            *ANALYSIS OF VARIANCE*  BIOMASS EARLY 1979 (T1)
CAUTION: BOTTOM LINE ERROR MEAN SQUARE MAY NOT BE APPROPRIATE FOR F-TEST
--------------------------------------------------------------------------------
  SOURCE        D.F.          SUM OF SQUARES              MEAN SQUARE
--------------------------------------------------------------------------------
 S                 3           85033.87500               28344.62500
 R                 2          395181.93750              197590.93750
 SR                6          365637.68750               60939.61328
COV 1              1           51420.73438               51420.73438
COV 3              1           10278.17969               10278.17969
COV 4              1            1628.55933                1628.55933
COV 5              1             706.84985                 706.84985
    ERROR        116           42545.21875                 366.76904
--------------------------------------------------------------------------------
    TOTAL        131         1372868.00000               10479.90625
                             *ANALYSIS OF VARIANCE* BIOMASS LATE 1979 (T2)
--------------------------------------------------------------------------------
  SOURCE        D.F.          SUM OF SQUARES              MEAN SQUARE
--------------------------------------------------------------------------------
 S                 3         1528921.00000              509640.31250
 R                 2         3274949.00000             1637474.00000
 SR                6         3571942.00000              595323.62500
COV 1              1          874455.43750              874455.43750
COV 3              1             268.99170                 268.99170
COV 4              1           82212.06250               82212.06250
COV 5              1            6670.24219                6670.24219
    ERROR        116          178739.43750                1540.85716
--------------------------------------------------------------------------------
    TOTAL        131        14897920.00000              113724.56250
                      *ANALYSIS OF VARIANCE*   BIOMASS EARLY 1980 (T3)
--------------------------------------------------------------------------------
  SOURCE        D.F.          SUM OF SQUARES              MEAN SQUARE
--------------------------------------------------------------------------------
 S                 3         1308593.00000              436197.62500
 R                 2          127749.62500               63874.81250
 SR                6         3177832.00000              529638.62500
COV 1              1           72736.37500               72736.37500
COV 3              1           86820.68750               86820.68750
COV 4              1           14671.68359               14671.68359
COV 5              1            7093.68359                7093.68359
    ERROR        140           61248.86719                 437.49170
--------------------------------------------------------------------------------
    TOTAL        155         7432578.00000               47952.11328
                        *ANALYSIS OF VARIANCE* BIOMASS LATE 1980 (T4)
--------------------------------------------------------------------------------
  SOURCE        D.F.          SUM OF SQUARES              MEAN SQUARE
--------------------------------------------------------------------------------
 S                 3          643110.43750              214370.12500
 R                 2          479221.37500              239610.68750
 SR                5         3228298.00000              645659.56250
COV 1              1          126175.37500              126175.37500
COV 3              1           12412.05078               12412.05078
COV 4              1           20985.30078               20985.30078
COV 5              1            2440.82690                2440.82690
    ERROR         84           57120.68750                 680.00806
--------------------------------------------------------------------------------
    TOTAL         98         6575021.00000               67092.00000
```

E. Palatability indices during the grazing periods.

An explanation of these indices appears in Chapter V.

	Day	Aspen	Rose	Rasp.	Snowb.
1979 E	1	0.68	1.16	1.12	0.20
	2	0.71	1.29	1.24	0.45
	3	0.34	1.48	0.72	0.15
	4	0.91	1.35	1.07	0.36
	5	0.72	1.31	1.29	0.39
	6	0.85	1.54	1.16	0.20
	7	0.78	1.82	1.49	0.42
	8	0.53	1.95	1.28	0.11
	9	0.79	2.86	1.29	0.23
	10		1.26	0.73	
	mean	0.70	1.56	1.16	0.30
1979 L	1	0.63	1.32	1.13	0.29
	2	0.77	0.82	1.53	0.89
	3	0.64	0.71	1.70	0.79
	4	0.53	0.31	1.77	0.79
	5	0.58	0.44	1.55	0.98
	6	0.35	0.41	1.11	1.32
	7	0.45	0.68	1.41	1.14
	8	0.32	0.46	0.87	1.49
	9			1.10	0.88
	10	0.20		0.44	1.37
	mean	0.50	0.64	1.30	1.00
1980 E	1		1.24	0.62	
	2	0.21	1.73	2.78	0.23
	3	0.46	1.28	1.17	1.69
	4	0.34	1.23	2.98	0.19
	5	0.60	1.14	1.43	1.78
	6	0.80	1.56	1.79	0.26
	7	0.56	1.67	3.05	0.13
	8	0.56	0.23	2.21	0.94
	9	0.73	1.00		1.76
	10		1.00		
	11	1.00			1.35
	12				1.00
	mean	0.57	1.29	2.15	0.94
1980 L	1	1.19	0.90	1.07	0.41
	2	2.05	0.29	1.13	0.32
	3	2.21	0.30	1.04	0.46
	4	3.74	0.28	1.21	0.78
	5	1.64	0.23	1.35	0.75
	6	1.83	0.27	0.84	0.84
	7	2.37	0.47	0.58	1.09
	mean	2.09	0.39	1.05	0.71

F. Shoot morphology for 4 clipping treatments.

These data are for shoots grown on excised roots in three light regimes, and measured at harvest at termination of those regimes.

	Time of clipping				
	Nil	July 17	Aug. 7	Aug. 27	S.E.
Leaf area (cm^2 shoot^{-1})	7.3	7.3	6.6	8.2	4.8
Leaf wt. (mg root^{-1})	148	196	193	130	70.4
Leaf wt. (mg cm^{-2})	7.5	9.2	6.6	8.0	3.0
Av. shoot length (mm)	63	49	41	55	35.4
Stem wt (mg root^{-1})	123	129	70	75	70.0
Stem wt (mg mm^{-1})	0.40	0.47	0.30	0.41	0.25
Leaf:stem	1.8	1.8	2.1	1.8	0.35
Shoot wt. (mg root^{-1})	222	260	204	161	119
New root wt. (mg)	13.8	39.3	16.7	14.1	25.3
Shoot:root†	16.1	6.6	12.2	11.4	21.0

† arithmetic means.